

VII. *On the Structure and Development of Lepidosteus.*

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Received November 24,—Read December 8, 1881.

[PLATES 21-29.]

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INTRODUCTION.

THE following paper is the outcome of the very valuable gift of a series of embryos and larvæ of *Lepidosteus* by Professor ALEX. AGASSIZ, to whom we take this opportunity of expressing our most sincere thanks. The skull of these embryos and larvæ has been studied by Professor PARKER, and forms the subject of a memoir already presented to the Royal Society.

Considering that *Lepidosteus* is one of the most interesting of existing Ganoids, and that it is very closely related to species of Ganoids which flourished during the Triassic period, we naturally felt keenly anxious to make the most of the opportunity of working at its development offered to us by Professor AGASSIZ' gift. Professor AGASSIZ, moreover, most kindly furnished us with four examples of the adult Fish, which have enabled us to make this paper a study of the adult anatomy as well as of the development.

The first part of our paper is devoted to the segmentation, formation of the germinal layers, and general development of the embryo and larva. The next part consists of a series of sections on the organs, in which both their structure in the adult and their development are dealt with. This part is not, however, in any sense a monograph, and where already known, the anatomy is described with the greatest possible brevity. In this part of the paper considerable space is devoted to a comparison of the organs of *Lepidosteus* with those of other Fishes, and to a statement of the conclusions which follow from such comparison.

The last part of the paper deals with the systematic position of *Lepidosteus* and of the Ganoids generally.

GENERAL DEVELOPMENT.

The spawning of *Lepidosteus* takes place in the neighbourhood of New York about May 20th. AGASSIZ (No. 1)* gives an account of the process from Mr. S. W. GARMAN'S notes, which we venture to quote in full.

"Black Lake is well stocked with Bill-fish. When they appear, they are said to come in countless numbers. This is only for a few days in the spring, in the spawning season, between the 15th of May and the 8th of June. During the balance of the season they are seldom seen. They remain in the deeper parts of the lake, away from the shore, and, probably, are more or less nocturnal in habits. Out of season, an occasional one is caught on a hook baited with a Minnow. Commencing with the 20th of April, until the 14th of May we were unable to find the Fish, or to find persons who had seen them during this time. Then a fisherman reported having seen one rise to the surface. Later, others were seen. On the afternoon of the 18th, a few were found on the *points*, depositing the spawn. The temperature at the time was 68° to 69°

* The numbers refer to the list of memoirs of the anatomy and development given at the end of this memoir (p. 433).

on the shoals, while out in the lake the mercury stood at 62° to 63°. The *points* on which the eggs were laid were of naked granite, which had been broken by the frost and heat into angular blocks of 3 to 8 inches in diameter. The blocks were tumbled upon each other like loose heaps of brickbats, and upon and between them the eggs were dropped. The *points* are the extremities of small capes that make out into the lake. The eggs were laid in water varying in depth from 2 to 14 inches. At the time of approaching the shoals, the Fish might be seen to rise quite often to the surface to take air. This they did by thrusting the bill out of the water as far as the corners of the mouth, which was then opened widely and closed with a snap. After taking the air, they seemed more able to remain at the surface. Out in the lake they are very timid, but once buried upon the shoals they become quite reckless as to what is going on about them. A few moments after being driven off, one or more of the males would return as if scouting. If frightened, he would retire for some time; then another scout would appear. If all promised well, the females, with the attendant males, would come back. Each female was accompanied by from one to four males. Most often, a male rested against each side, with their bills reaching up toward the back of her head. Closely crowded together, the little party would pass back and forth over the rocky bed they had selected, sometimes passing the same spot half-a-dozen times without dropping an egg, then suddenly would indulge in an orgasm; and, lashing and plashing the water in all directions with their convulsive movements, would scatter at the same instant the eggs and the sperm. This ended, another season of moving slowly back and forth was observed, to be in turn followed by another of excitement. The eggs were excessively sticky. To whatever they happened to touch, they stuck, and so tenaciously that it was next to impossible to release them without tearing away a portion of their envelopes. It is doubtful whether the eggs would hatch if removed. As far as could be seen at the time, upon or under the rocks to which the eggs were fastened there was an utter absence of anything that might serve as food for the young Fishes.

“Other Fishes, Bull-heads, &c., are said to follow the Bill-fish to eat the spawn. It may be so. It was not verified. Certainly the points under observations were unmolested. During the afternoon of the 18th of May a few eggs were scattered on several of the beds. On the 19th there were more. With the spear and the snare, several dozens of both sexes of the Fish were taken. Taking one out did not seem greatly to startle the others. They returned very soon. The males are much smaller than the average size of the females; and, judging from those taken, would seem to have as adults greater uniformity in size. The largest taken was a female, of 4 feet 1½ inch in length. Others of 2 feet 6 inches contained ripe ova. With the 19th of May all disappeared, and for a time—the weather being meanwhile cold and stormy—there were no signs of their continued existence to be met with. Nearly two weeks later, on the 31st of May, as stated by Mr. HENRY J. PERRY, they again came up, not in small detachments on scattered points as before, but in multitudes, on every

shoal at all according with their ideas of spawning beds. They remained but two days. During the summer it happens now and then that one is seen to come up for his mouthful of air; beyond this there will be nothing to suggest the ravenous masses hidden by the darkness of the waters."

Egg membranes.—The ova of *Lepidosteus* are spherical bodies of about 3 millims. in diameter. They have a double investment consisting of (1) an outer covering formed of elongated, highly refractive bodies, somewhat pyriform at their outer ends (Plate 21, fig. 17, *f.e.*), which are probably metamorphosed follicular cells,* and (2) of an inner membrane, divided into two zones, viz.: an outer and thicker zone, which is radially striated, and constitutes the *zona radiata* (*z.r.*), and an inner and narrow homogeneous zone (*z.r'*).

Segmentation.—We have observed several stages in the segmentation, which show that it is complete, but that it approaches the meroblastic type more nearly than in the case of any other known holoblastic ovum.

Our earliest stage showed a vertical furrow at the upper or animal pole, extending through about one-fifth of the circumference (Plate 21, fig. 1), and in a slightly later stage we found a second similar furrow at right angles to the first (Plate 21, fig. 2). We have not been fortunate enough to observe the next phases of the segmentation, but on the second day after impregnation (Plate 21, fig. 3), the animal pole is completely divided into small segments, which form a disc, homologous to the blastoderm of meroblastic ova; while the vegetative pole, which subsequently forms a large yolk-sac, is divided by a few vertical furrows, four of which nearly meet at the pole opposite the blastoderm (Plate 21, fig. 4). The majority of the vertical furrows extend only a short way from the edge of the small spheres, and are partially intercepted by imperfect equatorial furrows.

Development of the embryo.—We have not been able to work out the stages immediately following the segmentation, owing to want of material; and in the next stage satisfactorily observed, on the third day after impregnation, the body of the embryo is distinctly differentiated. The lower pole of the ovum is then formed of a mass in which no traces of the previous segments or segmentation furrows could any longer be detected.

Some of the dates of the specimens sent to us appear to have been transposed; so that our statements as to ages must only be taken as *approximately* correct.

Third day after impregnation.—In this stage the embryo is about 3.5 millims. in length, and has a somewhat dumb-bell shaped outline (Plate 21, fig. 5). It consists

* We have examined the structure of the ovarian ova in order to throw light on the nature of these peculiar pyriform bodies. Unfortunately, the ovaries of our adult examples of *Lepidosteus* were so badly preserved, that we could not ascertain anything on this subject. The ripe ova in the ovary have an investment of pyriform bodies similar to those of the just laid ova.

With reference to the structure of the ovarian ova we may state that the germinal vesicles are provided with numerous nucleoli arranged in close proximity with the membrane of the vesicle.

of (1) an outer area (*p.z.*) with some resemblance to the area pellucida of the Avian embryo, forming the parietal part of the body; and (2) a central portion consisting of the vertebral and medullary plates and the axial portions of the embryo. In hardened specimens the peripheral part forms a shallow depression surrounding the central part of the embryo.

The central part constitutes a somewhat prominent ridge, the axial part of it being the medullary plate. Along the anterior half of this part a dark line could be observed in all our specimens, which we at first imagined to be caused by a shallow groove. We have, however, failed to find in our sections a groove in this situation except in a single instance (Plate 22, fig. 20, *x*), and are inclined to attribute the appearance above-mentioned to the presence of somewhat irregular ridges of the outer layer of the epiblast, which have probably been artificially produced in the process of hardening.

The anterior end of the central part is slightly dilated to form the brain (*b.*); and there is present a pair of lateral swellings near the anterior end of the brain which we believe to be the commencing optic vesicles. We could not trace any other clear indications of the differentiation of the brain into distinct lobes.

At the hinder end of the central part of the embryo a very distinct dilatation may also be observed, which is probably homologous with the tail swelling of Teleostei. Its structure is more particularly dealt with in the description of our sections of this stage.

After the removal of the egg-membranes described above we find that there remains a delicate membrane closely attached to the epiblast. This membrane can be isolated in distinct portions, and appears to be too definite to be regarded as an artificial product.

We have been able to prepare several more or less complete series of sections of embryos of this stage (Plate 22, figs. 18–22). These sections present as a whole a most striking resemblance to those of Teleostean embryos at a corresponding stage of development.

Three germinal layers are already fully established. The epiblast (*ep.*) is formed of the same parts as in Teleostei, viz. :—of an outer epidermic and an inner nervous or mucous stratum. In the parietal region of the embryo these strata are each formed of a single row of cells only. The cells of both strata are somewhat flattened, but those of the epidermic stratum are decidedly the more flattened of the two.

Along the axial line there is placed, as we have stated above, the medullary plate. The epidermic stratum passes over this plate without undergoing any change of character, and the plate is *entirely constituted of the nervous stratum of the epidermis*.

The medullary plate has, roughly speaking, the form of a solid keel, projecting inwards towards the yolk. There is no trace, at this stage at any rate, of a medullary groove; and as we shall afterwards show, the central canal of the cerebro-spinal cord is formed in the middle of the solid keel. The shape of this keel varies according to

the region of the body. In the head (Plate 22, fig. 18, *m.c.*), it is very prominent, and forming, as it does, the major part of the axial tissue of the body, impresses its own shape on the other parts of the head and gives rise to a marked ridge on the surface of the head directed towards the yolk. In the trunk (Plate 22, figs. 19, 20) the keel is much less prominent, but still projects sufficiently to give a convex form to the surface of the body turned towards the yolk.

In the head, and also near the hind end of the trunk, the nervous layer of the epiblast continuous with the keel on each side is considerably thicker than the lateral parts of the layer. The thickening of the nervous layer in the head gives rise to what has been called by GÖTTE* "the special sense plate," owing to its being subsequently concerned in the formation of parts of the organs of special sense. We cannot agree with GÖTTE in regarding it as part of the brain.

In the keel itself two parts may be distinguished, viz.: a superficial part, best marked in the region of the brain, formed of more or less irregularly arranged polygonal cells, and a deeper part of horizontally placed flatter cells. The upper part is mainly concerned in the formation of the cranial nerves, and of the dorsal roots of the spinal nerves.

The mesoblast (*ms.*) in the trunk consists of a pair of independent plates which are continued forwards into the head, and in the prechordal region of the latter, unite below the medullary keel.

The mesoblastic plates of the trunk are imperfectly divided into vertebral and lateral regions. Neither longitudinal sections nor surface views show at this stage any trace of a division of the mesoblast into somites. The mesoblast cells are polygonal, and no indication is as yet present of a division into splanchnic and somatic layers.

The notochord (*nc.*) is well established, so that its origin could not be made out. It is, however, much more sharply separated from the mesoblastic plates than from the hypoblast, though the ventral and inner corners of the mesoblastic plates which run in underneath it on either side, are often imperfectly separated from it. It is formed of polygonal cells, of which between 40 and 50 may as a rule be seen in a single section. No sheath is present around it. It has the usual extension in front.

The hypoblast (*hy.*) has the form of a membrane, composed of a single row of oval cells, bounding the embryo on the side adjoining the yolk.

In the region of the caudal swelling the relations of the germinal layers undergo some changes. This region may, from the analogy of other Vertebrates, be assumed to constitute the lip of the blastopore. We find accordingly that the layers become more or less fused. In the anterior part of the tail swelling, the boundary between the notochord and hypoblast becomes indistinct. A short way behind this point (Plate 22, fig. 21), the notochord unites with the medullary keel, and a neurenteric

* "Üb. d. Entwickl. d. Central-Nerven Systems d. Teleostier," Archiv für mikr. Anat., vol. xv., 1873.

cord, homologous with the neurenteric canal of other Ichthyopsida, is thus established. In the same region the boundary between the lateral plates of mesoblast and the notochord, and further back (Plate 22, fig. 22), that between the mesoblast and the medullary keel, becomes obliterated.

Fifth day after impregnation.—Between the stage last described and the next stage of which we have specimens, a considerable progress has been made. The embryo (Plate 21, figs. 6 and 7) has grown markedly in length and embraces more than half the circumference of the ovum. Its general appearance is, however, much the same as in the earlier stage, but in the cephalic region the medullary plate is divided by constrictions into three distinct lobes, constituting the regions of the fore-brain, the mid-brain, and the hind-brain. The fore-brain (Plate 21, fig. 6, *f.b.*) is considerably the largest of the three lobes, and a pair of lateral projections forming the optic vesicles are decidedly more conspicuous than in the previous stage. The mid-brain (*m.b.*) is the smallest of the three lobes, while the hind-brain (*h.b.*) is decidedly longer, and passes insensibly into the spinal cord behind.

The medullary keel, though retaining to a great extent the shape it had in the last stage, is no longer completely solid. Throughout the whole region of the brain and in the anterior part of the trunk (Plate 22, figs. 23, 24, 25) a slit-like lumen has become formed. We are inclined to hold that this is due to the appearance of a space between the cells, and not, as supposed by OELLACHER for Teleostei, to an actual absorption of cells, though we must admit that our sections are hardly sufficiently well preserved to be conclusive in settling this point. Various stages in its growth may be observed in different regions of the cerebro-spinal cord. When first formed, it is a very imperfectly defined cavity, and a few cells may be seen passing right across from one side of it to the other. It gradually becomes more definite, and its wall then acquires a regular outline.

The optic vesicles are now to be seen in section (Plate 22, fig. 23, *op.*) as flattish outgrowths of the wall of the fore-brain, into which the lumen of the third ventricle is prolonged for a short distance.

The brain has become to some extent separate from the superjacent epiblast, but the exact mode in which this is effected is not clear to us. In some sections it appears that the separation takes place in such a way that the nervous keel is only covered above by the epidermic layer of the epiblast, and that the nervous layer, subsequently interposed between the two, grows in from the two sides. Such a section is represented in Plate 22, fig. 24. Other sections again favour the view that in the isolation of the nervous keel, a superficial layer of it remains attached to the nervous layer of the epidermis at the two sides, and so, from the first, forms a continuous layer between the nervous keel and the epidermic layer of the epiblast (Plate 22, fig. 25). In the absence of a better series of sections we do not feel able to determine this point. The posterior part of the nervous keel retains the characters of the previous stage.

At the sides of the hind-brain very distinct commencements of the auditory vesicles are

apparent. They form shallow pits (Plate 22, fig. 24, *au.*) of the thickened part of the nervous layer adjoining the brain in this region. Each pit is covered over by the epidermic layer above, which has no share in its formation.

In many parts of the lateral regions of the body the nervous layer of the epidermis is more than one cell deep.

The mesoblastic plates are now divided in the anterior part of the trunk into a somatic and a splanchnic layer (Plate 22, fig. 25, *so.*, *sp.*), though no distinct cavity is as yet present between these two layers. Their vertebral extremities are somewhat wedge-shaped in section, the base of the wedge being placed at the sides of the medullary keel. The wedge-shaped portions are formed of a superficial layer of palisade-like cells and an inner kernel of polygonal cells. The superficial layer on the dorsal side is continuous with the somatic mesoblast, while the remainder pertains to the splanchnic layer.

The diameter of the notochord has diminished, and the cells have assumed a flattened form, the protoplasm being confined to an axial region. In consequence of this, the peripheral layer appears clear in transverse sections. A delicate cuticular sheath is formed around it. This sheath is probably the commencement of the permanent sheath of later stages, but at this stage it cannot be distinguished in structure from a delicate cuticle which surrounds the greater part of the medullary cord.

The hypoblast has undergone no changes of importance.

The layers at the posterior end of the embryo retain the characters of the last stage.

Sixth day after impregnation.—At this stage (Plate 21, fig. 8) the embryo is considerably more advanced than at the last stage. The trunk has decidedly increased in length, and the head forms a relatively smaller portion of the whole. The regions of the brain are more distinct. The optic vesicles (*op.*) have grown outwards so as to nearly reach the edges of the area which forms the parietal part of the body. The fore-brain projects slightly in front, and the mid-brain is seen as a distinct rounded prominence. Behind the latter is placed the hind-brain, which passes insensibly into the spinal cord. On either side of the mid- and hind-brain a small region is slightly marked off from the rest of the parietal part, and on this are seen two more or less transversely directed streaks, which, by comparison with the Sturgeon,* we are inclined to regard as the two first visceral clefts (*br.c.*). We have, however, failed to make them out in sections, and owing to the insufficiency of our material, we have not even studied them in surface views as completely as we could have wished.

The body is now laterally compressed, and more decidedly raised from the yolk than in the previous stages. In the lateral regions of the trunk the two segmental or archinephric ducts (*sg.*) are visible in surface views: the front end of each is placed at the level of the hinder border of the head, and is marked by a flexure inwards towards the middle line. The remainder of each duct is straight, and extends

* SALENSKY, "Recherches s. le Développement du Sterlet." Archives de Biol., vol. ii., 1881, pl. xvii., fig. 27.

backwards for about half the length of the embryo. The tail has much the same appearance as in the last stage.

The vertebral regions of the mesoblastic plates are now segmented for the greater part of the length of the trunk, and the somites of which they are composed (Plate 23, fig. 30, *pr.*) are very conspicuous in surface views.

Our sections of this stage are not so complete as could be desired: they show, however, several points of interest.

The central canal of the nervous system is large, with well-defined walls, and in hardened specimens is filled with a coagulum. It extends nearly to the region of the tail.

The optic vesicles, which are so conspicuous in surface views, appear in section (Plate 22, fig. 26, *op.*) as knob-like outgrowths of the fore-brain, and very closely resemble the figures given by OELLACHER of these vesicles in Teleostei.*

From the analogy of the previous stage, we are inclined to think that they have a lumen continuous with that of the fore-brain. In our only section through them, however, they are solid, but this is probably due to the section merely passing through them to one side.

The auditory pits (Plate 22, fig. 27, *au.*) are now well marked, and have the form of somewhat elongated grooves, the walls of which are formed of a single layer of columnar cells belonging to the nervous layer of the epidermis, and extending inwards so as nearly to touch the brain.

In an earlier stage it was pointed out that the dorsal part of the medullary keel was different in its structure from the remainder, and that it was destined to give rise to the nerves. The process of differentiation is now to a great extent completed, and may best be seen in the auditory region (Plate 22, fig. 27, VIII.). In this region there was present during the last stage a great rhomboidal mass of cells at the dorsal region of the brain (Plate 22, fig. 24, VIII.). In the present stage, this, which is the rudiment of the seventh and auditory nerves, is seen growing down on each side from the roof of the hind-brain, between the brain and the auditory involution, and abutting against the wall of the latter.

Rudiments of the spinal nerves are also seen at intervals as projections from the dorsal angles of the spinal cord (Plate 23, fig. 29, *sp.n.*). They extend only for a short distance outwards, gradually tapering off to a point, and situated between the epiblast and the dorsal angles of the mesoblastic somites.

The process of formation of the cranial nerves and dorsal roots of the spinal nerves is, it will be seen, essentially the same as that already known in the case of Elasmobranchii, Aves, &c. The nerves arise as outgrowths of a special crest of cells, the *neural crest* of MARSHALL, which is placed along the dorsal angle of the cord. The peculiar position of the dorsal roots of the spinal nerves is also very similar to what has been met

* "Beiträge zur Entwick. d. Knochenfische," Zeit. f. wiss. Zool., vol. xxiii., 1873, taf. iii., fig. ix., 2.

with in the early stages of these structures by MARSHALL in Birds,* and by one of us in Elasmobranchs.†

In the parietal region a cavity has now appeared in part of the trunk between the splanchnic and somatic layers of the mesoblast (Plate 23, fig. 29, *b.c.*), the somatic layer (*so.*) consisting of a single row of columnar cells on the dorsal side, while the remainder of each somite is formed of the splanchnic layer (*sp.*). In many of the sections the somatic layer is separated by a considerable interval from the epiblast.

We have been able to some extent to follow the development of the segmental duct. The imperfect preservation of our specimens has, as in other instances, rendered the study of the point somewhat difficult, but we believe that the figure representing the development of the duct some way behind its front end (Plate 23, fig. 29) is an accurate representation of what may be seen in a good many of our sections.

It appears from these sections that the duct (Plate 23, fig. 29, *sg.*) is developed as a hollow ridge-like outgrowth of the somatic layer of mesoblast, directed towards the epiblast, in which it causes a slight bulging. The cavity of the ridge freely communicates with the body-cavity. The anterior part of this ridge appears to be formed first. Very soon, in fact, in an older embryo belonging to this stage, the greater part of the groove becomes segmented off as a duct lying between the epiblast and somatic mesoblast (Plate 23, fig. 28, *sg.*), while the front end still remains, as we believe, in communication with the body cavity by an anterior pore.

This mode of development corresponds in every particular with that observed in Teleostei by ROSENBERG and OELLACHER.

The structure of the notochord (*nc.*) at this stage is very similar to that observed by one of us in Elasmobranchii.‡ The cord is formed of transversely arranged flattened cells, the outer parts of which are vacuolated, while the inner parts are granular, and contain the nuclei. This structure gives rise to the appearance in transverse sections of an axial darker area and a peripheral lighter portion.

The hypoblast retains for the most part its earlier constitution, but underneath the notochord, in the trunk, it is somewhat thickened, and the cells at the two sides spread in to some extent under the thickened portion (Plate 23, fig. 29, *s.nc.*). This thickening, as is shown in transverse sections at the stage when the segmental duct becomes separated from the somatic mesoblast (Plate 23, fig. 28, *s.nc.*), is the commencement of the subnotochordal rod.

The tail end of the embryo still retains its earlier characters.

Seventh day after impregnation.—Our series of specimens of this stage is very imperfect, and we are only able to call attention to the development of a certain number of organs.

Our sections clearly establish the fact that the optic vesicles are now hollow processes

* Journal of Anat. and Physiol., vol. xi., p. 491, plates xx. and xxi.

† 'Elasmobranch Fishes,' p. 156, plates x. and xiii.

‡ Ibid., p. 136, plate xi., fig. 10.

of the fore-brain. Their outer ends are dilated, and are in contact with the external skin. The formation of the optic cup has not, however, commenced. The nervous layer of the skin adjoining the outer wall of the optic cup is very slightly thickened, constituting the earliest rudiment of the lens.

In one of our embryos of this day the developing auditory vesicle still has the form of a pit, but in the other it is a closed vesicle, already constricted off from the nervous layer of the epidermis.

With reference to the development of the excretory duct we cannot add much to what we have already stated in describing the last stage.

The duct is considerably dilated anteriorly (Plate 23, fig. 31, *sg.*); but our sections throw no light on the nature of the abdominal pore. The posterior part of the duct has still the form of a hollow ridge united with somatic mesoblast (Plate 23, fig. 32, *sg.*).

During this stage, the embryo becomes to a small extent folded off from the yolk-sac both in front and behind, and in the course of this process the anterior and posterior extremities of the alimentary tract become definitely established.

We have not got as clear a view of the process of formation of these two sections of the alimentary tract as we could desire, but our observations appear to show that the process is in many respects similar to that which takes place in the formation of the anterior part of the alimentary tract in Elasmobranchii.* One of us has shown that in Elasmobranchs the ventral wall of the throat is formed *not* by a process of folding in of the hypoblastic sheet as in Birds, but by a growth of the ventral face of the hypoblastic sheet on each side of and at some little distance from the middle line. Each growth is directed inwards, and the two eventually meet and unite, thus forming a complete ventral wall for the gut. Exactly the same process would seem to take place in *Lepidosteus*, and after the lumen of the gut is in this way established, a process of mesoblast on each side also makes its appearance, forming a mesoblastic investment on the ventral side of the alimentary tract. Some time after the alimentary tract has been thus formed, the epiblast becomes folded in, in exactly the same manner as in the Chick, the embryo becoming thereby partially constricted off from the yolk (Plate 23, figs. 33, 34).

The form of the lumen of the alimentary tract differs somewhat in front and behind. In front, the hypoblastic sheet remains perfectly flat during the formation of the throat, and thus the lumen of the latter has merely the form of a slit. The lumen of the posterior end of the alimentary tract is, however, narrower and deeper (Plate 23, figs. 33, 34, *al.*). Both in front and behind, the lateral parts of the hypoblastic sheet become separated from the true alimentary tract as soon as the lumen of the latter is established.

It is quite possible that at the extreme posterior end of the embryo a modification of the above process may take place, for in this region the hypoblast appears to us to have the form of a solid cord.

* F. M. BALFOUR, 'Monograph on the Development of Elasmobranch Fishes,' p. 87, plate ix., fig. 2.

We could detect no true neurenteric canal, although a more or less complete fusion of the germinal layers at the tail end of the embryo may still be traced.

During this stage the protoplasm of the notochordal cells, which in the last stage formed a kind of axial rod in the centre of the notochord, begins to spread outwards toward the sheath of the notochord.

Eighth day after impregnation.—The external form of the embryo (Plate 21, fig. 9) shows a great advance upon the stage last figured. Both head and body are much more compressed laterally and raised from the yolk, and the head end is folded off for some distance. The optic vesicles are much less prominent externally. A commencing opercular fold is distinctly seen. Our figure of this stage is not, however, so satisfactory as we could wish.

A thickening of the nervous layer of the external epiblast which will form the lens (Plate 23, fig. 35, *l.*) is more marked than in the last stage, and presses against the slightly concave exterior wall of the optic vesicle (*op.*). The latter has now a large cavity, and its stalk is considerably narrowed.

The auditory vesicles (Plate 23, fig. 36, *au.*) are closed, appearing as hollow sacs one on each side of the brain, and are no longer attached to the epiblast.

The anterior opening of the segmental duct can be plainly seen close behind the head. The lumen of the duct is considerably larger.

The two vertebral portions of the mesoblast are now separated by a considerable space from the epiblast on one side and from the notochord on the other, and the cells composing them have become considerably elongated from side to side (Plate 23, fig. 37, *ms.*).

In some sections the aorta can be seen (Plate 23, fig. 37, *ao.*) lying close under the sub-notochordal rod, between it and the hypoblast, and on either side of it a slightly larger cardinal vein (*cd.v.*).

The protoplasm of the notochord has now again retreated towards the centre, showing a clear space all round. This is most marked in the region of the trunk (Plate 23, fig. 37). The sub-notochordal rod (*s.nc.*) lies close under it.

A completely closed fore-gut, lined by thickened hypoblast, extends about as far back as the auditory sacs (Plate 23, figs. 35 and 36, *al.*). In the trunk the hypoblast, which will form the walls of the alimentary tract, is separated from the notochord by a considerable interval.

Ninth day after impregnation: External characters.—Very considerable changes have taken place in the external characters of the embryo. It is about 8 millims. in length, and has assumed a completely piscine form. The tail especially has grown in length, and is greatly flattened from side to side: it is wholly detached from the yolk, and bends round towards the head, usually with its left side in contact with the yolk. It is provided with well-developed dorsal and ventral fin-folds, which meet each other round the end of the tail, the tail fin so formed being nearly symmetrical. The head is not nearly so much folded off from the yolk as the tail. At its front end is placed a

disc with numerous papillæ, of which we shall say more hereafter. This disc is somewhat bifid, and is marked in the centre by a deep depression.

Dorsal to it, on the top of the head, are two widely separated nasal pits. On the surface of the yolk, in front of the head, is to be seen the heart, just as in Sturgeon embryos. Immediately below the suctorial disc is a slit-like space, forming the mouth. It is bounded below by the two mandibular arches, which meet ventrally in the median line. A shallow but well marked depression on each side of the head indicates the posterior boundary of the mandibular arch. Behind this is placed the very conspicuous hyoid arch with its rudimentary opercular flap; and in the depression, partly covered over by the latter, may be seen a ridge, the external indication of the first branchial arch.

Eleventh day after impregnation: External characters.—The embryo (Plate 21, fig. 10) is now about 10 millims. in length, and in several features exhibits an advance upon the embryo of the previous stage.

The tail fin is now obviously not quite symmetrical, and the dorsal fin-fold is continued for nearly the whole length of the trunk. The suctorial disc (Plate 21, fig. 11, *s.d.*) is much more prominent, and the papillæ (about 30 in number) covering it are more conspicuous from the surface. It is not obviously composed of two symmetrical halves. The opercular flap is larger, and the branchial arches behind it (two of which may be made out without dissection) are more prominent.

The anterior pair of limbs is now visible in the form of two *longitudinal* folds projecting in a vertical direction from the surface of the yolk-sac at the sides of the body.

The stages subsequent to hatching have been investigated with reference to the external features and to the habits by AGASSIZ, and we shall enrich our own account by copious quotations from his memoir.

He states that the first batch were hatched on the eighth* day after being laid. "The young Fish possessed a gigantic yolk-bag, and the posterior part of the body presented nothing specially different from the general appearance of a Teleostean embryo, with the exception of the great size of the chorda. The anterior part, however, was most remarkable; and at first, on seeing the head of this young *Lepidosteus*, with its huge mouth-cavity extending nearly to the gill-opening, and surmounted by a hoof-shaped depression edged with a row of protuberances acting as suckers, I could not help comparing this remarkable structure, so utterly unlike anything in Fishes or Ganoids, to the Cyclostomes, with which it has a striking analogy. This organ is also used by *Lepidosteus* as a sucker, and the moment the young Fish is hatched he attaches himself to the sides of the disc, and there remains hanging immovable; so firmly attached, indeed, that it requires considerable commotion in the water to make him loose his hold. Aerating the water by pouring it from a height did not always produce sufficient disturbance to loosen the young Fishes. The eye, in this stage, is

* This statement of AGASSIZ does not correspond with the dates on the specimens sent to us—a fact no doubt due to the hatching not taking place at the same time for all the larvæ.

rather less advanced than in corresponding stages in bony Fishes; the brain is also comparatively smaller, the otolith ellipsoidal, placed obliquely in the rear above the gill-opening. . . . Usually the gill-cover is pressed closely against the sides of the body, but in breathing an opening is seen through which water is constantly passing, a strong current being made by the rapid movement of the pectorals, against the base of which the extremity of the gill-cover is closely pressed. The large yolk-bag is opaque, of a bluish-gray colour. The body of the young *Lepidosteus* is quite colourless and transparent. The embryonic fin is narrow, the dorsal part commencing above the posterior end of the yolk-bag; the tail is slightly rounded, the anal opening nearer the extremity of the tail than the bag. The intestine is narrow, and the embryonic fin extending from the vent to the yolk-bag is quite narrow. In a somewhat more advanced stage,—hatched a few hours earlier,—the upper edge of the yolk-bag is covered with black pigment cells, and minute black pigment cells appear on the surface of the alimentary canal. There are no traces of embryonic fin-rays either in this stage or the one preceding; the structure of the embryonic fin is as in bony Fishes—previous to the appearance of these embryonic fin-rays—finely granular. Seen in profile, the yolk-bag is ovoid; as seen from above, it is flattened, rectangular in front, with rounded corners, tapering to a rounded point towards the posterior extremity, with re-entering sides.”

We have figured an embryo of 11 millims. in length, shortly after hatching (Plate 21, fig. 12), the most important characters of which are as follows:—The yolk-sac, which has now become much reduced, forms an appendage attached to the ventral surface of the body, and has a very elongated form as compared with its shape just before hatching. The mouth, as also noticed by AGASSIZ, has a very open form. It is (Plate 21, fig. 13, *m.*) more or less rhomboidal, and is bounded behind by the mandibular arch (*mn.*) and laterally by the superior maxillary processes (*s.mx.*). In front of the mouth is placed the suctorial disc (*s.d.*), the central papillæ of which are arranged in groups. The opercular fold (*h.op.*) is very large, covering the arches behind. A well-marked groove is present between the mandibular and opercular arches, but so far as we can make out it is not a remnant of the hyomandibular cleft.

The pectoral fins (Plate 21, fig. 12, *pc.f.*) are very prominent longitudinal ridges, which, owing to their being placed on the surface of the yolk-sac, project in a nearly vertical direction: a feature which is also found in many Teleostean embryos with large yolk-sacs.

No traces of the pelvic fins have yet become developed.

The positions of the permanent dorsal, anal, and caudal fins, as pointed out by AGASSIZ, are now indicated by a deposit of pigment in the embryonic fin.

In an embryo on the sixth day after hatching, of about 15 millims. in length, of which we have also given a figure (Plate 21, fig. 14), the following fresh features deserve special notice.

In the region of the head there is a considerable elongation of the pre-oral part, forming a short snout, at the end of which is placed the suctorial disc. At the sides of the snout are placed the nasal pits, which have become somewhat elongated anteriorly.

The mouth has lost its open rhomboidal shape, and has become greatly narrowed in an antero-posterior direction, so that its opening is reduced to a slit. The mandibles and maxillary processes are nearly parallel, though both of them are very much shorter than in the adult. The operculum is now a very large flap, and has extended so far backwards as to cover the insertion of the pectoral fin. The two opercular folds nearly meet ventrally.

The yolk-sac is still more reduced in size, one important consequence of which is that the pectoral fins (*pc.f.*) appear to spring out more or less horizontally from the sides of the body, and at the same time their primitive line of attachment to the body becomes transformed from a longitudinal to a more or less transverse one.

The first traces of the pelvic fins are now visible as slight longitudinal projections near the hinder end of the yolk-sac (*pl.f.*).

The pigmentation marking the regions of the permanent fins has become more pronounced, and it is to be specially noted that the ventral part of the caudal fin (the permanent caudal) is considerably more prominent than the dorsal fin opposite to it.

The next changes, as AGASSIZ points out, "are mainly in the lengthening of the snout; the increase in length both of the lower and upper jaw; the concentration of the sucker of the sucking disc; and the adoption of the general colouring of somewhat older Fish. The lobe of the pectoral has become specially prominent, and the outline of the fins is now indicated by a fine milky granulation. Seen from above, the gill-cover is seen to leave a large circular opening leading to the gill-arches, into which a current of water is constantly passing, by the lateral expansion and contraction of the gill-cover; the outer extremity of the gill-cover covers the base of the pectorals. In a somewhat older stage the snout has become more elongated, the sucker more concentrated, and the disproportionate size of the terminal sucking-disc is reduced; the head, when seen from above, becoming slightly elongated and pointed."

In a larva of about 18 days old and 21 millims. in length, of which we have not given a figure, the snout has grown greatly in length, carrying with it the nasal organs, the openings of which now appear to be divided into two parts. The suctorial disc is still a prominent structure at the end of the snout. The lower jaw has elongated correspondingly with the upper, so that the gape is very considerable, though still very much less than in the adult.

The opercular flaps overlap ventrally, the left being superficial. They still cover the bases of the pectoral fins. The latter are described by AGASSIZ as being "kept in constant rapid motion, so that the fleshy edge is invisible, and the vibration seems almost involuntary, producing a constant current round the opening leading into the cavity of the gills."

The pelvic fins are somewhat more prominent.

The yolk-sac, as pointed out by AGASSIZ, has now disappeared as an external appendage.

After the stage last described the young Fish rapidly approaches the adult form. To show the changes effected we have figured the head of a larva of about a month old and 23 millims. in length (Plate 21, fig. 15). The suctorial disc, though much reduced, is still prominent at the end of the snout. Eventually, as shown by AGASSIZ, it forms the fleshy globular termination of the upper jaw.

The most notable feature in which the larva now differs in its external form from the adult is in the presence of an externally heterocercal tail, caused by the persistence of the primitive caudal fin as an elongated filament projecting beyond the permanent caudal (Plate 28, fig. 68).

Delicate dermal fin-rays are now conspicuous in the peripheral parts of all the permanent fins. These rays closely resemble the horny fin-rays in the fins of embryo Elasmobranchs in their development and structure. They appear gradually to enlarge to form the permanent rays, and we have followed out some of the stages of their growth, which is in many respects interesting. Our observations are not, however, complete enough to publish, and we can only say here that their early development and structure proves their homology with the horny fibres or rays in fins of Elasmobranchii. The skin is still, however, entirely naked, and without a trace of its future armour of enamelled scales.

The tail of a much older larva, 11 centims. in length, in which the scales have begun to be formed, is shown in Plate 21, fig. 16.

We complete this section of our memoir by quoting the following passages from AGASSIZ as to the habits of the young fish at the stages last described :—

“In the stages intervening between plate iii, fig. 19, and plate iii, fig. 30, the young *Lepidosteus* frequently swim about, and become readily separated from their point of attachment. In the stage of plate iii, fig. 30, they remain often perfectly quiet close to the surface of the water; but, when disturbed, move very rapidly about through the water. . . . The young already have also the peculiar habit of the adult of coming to the surface to swallow air. When they go through the process under water of discharging air again they open their jaws wide, and spread their gill-covers, and swallow as if they were choking, making violent efforts, until a minute bubble of air has become liberated, when they remain quiet again. The resemblance to a Sturgeon in the general appearance of this stage of the young *Lepidosteus* is quite marked.”

BRAIN.

I. *Anatomy.*

The brain of *Lepidosteus* has been figured by BUSCH (whose figure has been copied by MIKLUCHO-MACLAY, and apparently by HUXLEY), by OWEN, and by WILDER

(No. 15). The figure of the latter author, representing a longitudinal section through the brain, is the most satisfactory, the other figures being in many respects inaccurate ; but even WILDER's figure and description, though taken from the fresh object, appears to us in some respects inadequate. He offers, moreover, fresh interpretations of certain parts of the brain which we shall discuss in the sequel.

We have examined two brains which, though extremely soft, were, nevertheless, sufficiently well preserved to enable us to study the external form. We have, moreover, made a complete series of transverse sections through one of the brains, and our sections, though utterly valueless from a histological point of view, have thrown some light on the topographical anatomy of the brain.

Plate 25, figs. 47 A, B, and C, represent three views of the brain, viz. : from the side, from above, and from below. We will follow in our description the usual division of the brain into fore-brain, mid-brain, and hind-brain.

The fore-brain consists of an anterior portion forming the cerebrum, and a posterior portion constituting the thalamencephalon.

The cerebrum at first sight appears to be composed of (*a*) a pair of posterior and somewhat dorsal lobes, forming what have usually been regarded as the true cerebral hemispheres, but called by WILDER the prothalami, and (*b*) a pair of anterior and ventral lobes, usually regarded as the olfactory lobes, from which the olfactory nerves spring. Mainly from a comparison with our embryonic brains described in the sequel, we are inclined to think that the usual interpretations are not wholly correct, but that the true olfactory lobes are to be sought for in small enlargements (Plate 25, figs. 47 A, B, and C, *olf.*) at the front end of the brain * from which the olfactory nerves spring. The cerebrum proper would then consist of a pair of anterior and ventral lobes (*ce.*), and of a pair of posterior lobes (*ce'.*), both pairs uniting to form a basal portion behind.

The two pairs of lobes probably correspond with the two parts of the cerebrum of the Frog, the anterior of which, like that of *Lepidosteus*, was held to be the olfactory lobe, till GÖTTE's researches showed that this view was not tenable.

The anterior lobes of the cerebrum have a conical form, tapering anteriorly, and are completely separated from each other. The posterior lobes, as is best shown in side views, have a semicircular form. Viewed from above they appear as rounded prominences, and their dorsal surface is marked by two conspicuous furrows (Plate 25, fig. 47 B, *ce'.*), which have been noticed by WILDER, and are similar to those present in many Teleostei. Their front ends overhang the base of the anterior cerebral lobes. The basal portion of the cerebrum is an undivided lobe, the anterior wall of which forms the lamina terminalis.

What we have above described as the posterior cerebral lobes have been described by WILDER as constituting the everted dorsal border of the basal portion of the cerebrum.

The portion of the cerebro-spinal canal within the cerebrum presents certain primitive characters, which are in some respects dissimilar to those of higher types,

* The homologies of the olfactory lobes throughout the group of Fishes require further investigation.

and have led WILDER to hold the posterior cerebral lobes, together with what we have called the basal portion of the cerebrum, to be structures peculiar to Fishes, for which he has proposed the name "prothalami."

In the basal portion of the cerebrum there is an unpaired slit-shaped ventricle, the outer walls of which are very thick. It is provided with a floor formed of nervous matter, in part of which, judging from WILDER's description, a well-marked commissure is placed. We have found in the larva a large commissure in this situation (Plate 24, figs. 44 and 45, *a.c.*); and it may be regarded as the homologue of the anterior commissure of higher types. This part of the ventricle is stated by WILDER to be without a roof. This appears to us highly improbable. We could not, however, determine the nature of the roof from our badly preserved specimens, but if present, there is no doubt that it is extremely thin, as indeed it is in the larva (Plate 24, fig. 46 B). In a dorsal direction the unpaired ventricle extends so as to separate the two posterior cerebral lobes. Anteriorly the ventricle is prolonged into two horns, which penetrate for a short distance, as *the lateral ventricles*, into the base of the anterior cerebral lobes. The front part of each anterior cerebral lobe, as well as of the whole of the posterior lobes, appears solid in our sections; but WILDER describes the anterior horns of the ventricle as being prolonged for the whole length of the anterior lobes.

In the embryos of all Vertebrates the cerebrum is not at first divided into two lobes, so that the fact of the posterior part of the cerebrum in *Lepidosteus* and probably other Ganoids remaining permanently in the undivided condition does not appear to us a sufficient ground for giving to the lobes of this part of the cerebrum the special name of prothalami, as proposed by WILDER, or for regarding them as a section of the brain peculiar to Fishes.

The thalamencephalon (*th.*) contains the usual parts, but is in some respects peculiar. Its lateral walls, forming the optic thalami, are thick, and are not sharply separated in front from the basal part of the cerebrum; between them is placed the third ventricle. The thalami are of considerable extent, though partially covered by the optic lobes and the posterior lobes of the cerebrum. They are not, however, relatively so large as in other Ganoid forms, more especially the Chondrostei and *Polypterus*.

On the roof of the thalamencephalon is placed a large thin-walled vesicle (Plate 25, figs. 47 A and B, *v.th.*), which undoubtedly forms the most characteristic structure connected with this part of the brain. Owing to the wretched state of preservation of the specimens, we have found it impossible to determine the exact relations of this body to the remainder of the thalamencephalon; but it appears to be attached to the roof of the thalamencephalon by a narrow stalk only. It extends forwards so as to overlap part of the cerebrum in front, and is closely invested by a highly vascular layer of the pia mater.

No mention is made by WILDER of this body; nor is it represented in his figures or in those of the other anatomists who have given drawings of the brain of *Lepidosteus*. It might at first be interpreted as a highly-developed pineal gland, but a comparison

with the brain of the larva (vide p. 378) shows that this is not the case, but that the body in question is represented in the larva by a special outgrowth of the roof of the thalamencephalon. The vesicle of the roof of the thalamencephalon is therefore to be regarded as a peculiar development of the tela choroidea of the third ventricle.

How far this vesicle has a homologue in the brains of other Ganoids is not certain, since negative evidence on this subject is all but valueless. It is possible that a vesicular sac covering over the third ventricle of the Sturgeon described by STANNIUS,* and stated by him to be wholly formed of the membranes of the brain, is really the homologue of our vesicle.

WIEDERSHEIM† has recently described in *Protopterus* a body which is undoubtedly homologous with our vesicle, which he describes in the following way :—

“Dorsalwärts ist das Zwischenhirn durch ein tiefes, von Hirnschlitz eingenommenes Thal von Vorderhirn abgesetzt; dasselbe ist jedoch durch eine häutige, mit der Pia mater zusammenhängende Kuppel oder Kapsel überbrückt.”

This “Kuppel” has precisely the same relations and a very similar appearance to our vesicle. The true pineal gland is placed behind it. It appears to us possible that the body found by HUXLEY‡ in *Ceratodus*, which he holds to be the pineal gland, is in reality this vesicle. It is moreover possible that what has usually been regarded as the pineal gland in *Petromyzon* may in reality be the homologue of the vesicle we have found in *Lepidosteus*.

We have no observations on the pineal gland of the adult, but must refer the reader for the structure and relations of this body to the embryological section.

The infundibulum (Plate 25, fig. 47 A, *in.*) is very elongated. Immediately in front of it is placed the optic chiasma (Plate 25, figs. 47 A and C, *op.ch.*) from which the optic fibres can be traced passing along the sides of the optic thalami and to the optic lobes, very much as in MÜLLER’S figure of the brain of *Polypterus*.

On the sides of the infundibulum are placed two prominent bodies, the lobi inferiores (*l.in.*), each of which contains a cavity continuous with the prolongation of the third ventricle into the infundibulum. The apex of the infundibulum is enlarged, and to it is attached a pituitary body (*pt.*).

The mid-brain is of considerable size, and consists of a basal portion connecting the optic thalami with the medulla, and a pair of large optic lobes (*op.l.*). The iter a tertio ad quartum ventriculum, which forms the ventricle of this part of the brain, is prolonged into each optic lobe, and the floor of each prolongation is taken up by a dome-shaped projection, the homologue of the torus semicircularis of Teleostei.

* “Üb. d. Gehirns des Stors,” MÜLLER’S Archiv., 1843, and Lehrbuch d. vergl. Anat. d. Wirbelthiere. CATTIE (Archives de Biologie, vol. iii., 1882, has recently described in *Acipenser sturio* a vesicle on the roof of the thalamencephalon, whose cavity is continuous with the third ventricle. This vesicle is clearly homologous with that in *Lepidosteus*. (June 28, 1882.)

† R. WIEDERSHEIM, ‘Morphol. Studien,’ 1880, p. 71.

‡ “On *Ceratodus Forsteri*,” &c., Proc. Zool. Soc., 1876.

The hind-brain consists of the usual parts, the medulla oblongata and the cerebellum. The medulla presents no peculiar features. The sides of the fourth ventricle are thickened and everted, and marked with peculiar folds (Plate 25, figs. 47 A and B, *m.o.*).

The cerebellum is much larger than in the majority of Ganoids, and resembles in all essential features the cerebellum of Teleostei. In side views it has a somewhat S-shaped form, from the presence of a peculiar lateral sulcus (Plate 25, fig. 47 A, *cb.*). As shown by WILDER, its wall actually has in longitudinal section this form of curvature, owing to its anterior part projecting forwards into the cavity of the iter.* This forward projection is not, however, so conspicuous as in most Teleostei. The cerebellum contains a large unpaired prolongation of the fourth ventricle.

II. *Development.*

The early development of the brain has already been described; and, although we do not propose to give any detailed account of the later stages of its growth, we have thought it worth while calling attention to certain developmental features which may probably be regarded as to some extent characteristic of the Ganoids. With this view we have figured (Plate 24, figs. 44, 45) longitudinal sections of the brain at two stages, viz.: of larvæ of 15 and 26 millims., and transverse sections (Plate 24, figs. 46 A-G) of the brain of a larva at about the latter stage (25 millims.).

The original embryonic fore-brain is divided in both embryos into a cerebrum (*ce.*) in front and a thalamencephalon (*th.*) behind. In the younger embryo the cerebrum is a single lobe, as it is in the brains of all Vertebrate embryos; but in the older larva it is anteriorly (Plate 24, fig. 46 A) completely divided into two hemispheres. The roof of the undivided posterior part of the cerebrum is extremely thin (Plate 24, fig. 46 B). Near the posterior border of the base of the cerebrum there is a great development of nervous fibres, which may probably be regarded as in part equivalent to the anterior commissure (Plate 24, figs. 44, 45, *a.c.*).

Even in the oldest of the two brains the olfactory lobes are very slightly developed, constituting, however, small lateral and ventral prominences of the front end of the hemispheres. From each of them there springs a long olfactory nerve, extending for the whole length of the rostrum to the olfactory sac.

The thalamencephalon presents a very curious structure, and is relatively a more important part of the brain than in the embryo of any other form which we know of. Its roof, instead of being, as usual, compressed antero-posteriorly,† so as to be almost concealed between the cerebral hemispheres and the optic lobes (mid-brain), projects on the surface for a length quite equal to that of the cerebral hemispheres (Plate 24, figs. 44 and 45, *th.*). In the median line the roof of the thalamencephalon is thin and folded; at its posterior border is placed the opening of the small pineal gland. This body is a papilliform process of the nervous matter of the roof of this part of the brain, and instead

* In WILDER's figure the walls of the cerebellum are represented as much too thin.

† Vide F. M. BALFOUR, 'Comparative Embryology,' vol. ii., figs. 243 and 250.

of being directed forwards, as in most Vertebrate types, tends somewhat backwards, and rests on the mid-brain behind (Plate 24, figs. 44, 45, and 46 C and D, *pn.*). The roof of the thalamencephalon immediately in front of the pineal gland forms a sort of vesicle, the sides of which extend laterally as a pair of lobes, shown in transverse sections in Plate 24, figs. 46 C and D, as *th.l.* This vesicle becomes, we cannot doubt, the vesicle on the roof of the thalamencephalon which we have described in the adult brain. Immediately in front of the pineal gland the roof of the thalamencephalon contains a transverse commissure (Plate 24, fig. 46 C, *z.*), which is the homologue of a similarly situated commissure present in the Elasmobranch brain,* while behind the pineal gland is placed the posterior commissure. The sides of the thalamencephalon are greatly thickened, forming the optic thalami (Plate 24, figs. 46 C and D, *op.th.*), which are continuous in front with the thickened outer walls of the hemispheres. Below, the thalamencephalon is produced into a very elongated infundibulum (Plate 24, figs. 44, 45, 46 E, *in.*), the apex of which is trilobed as in Elasmobranchii and Teleostei. The sides of the infundibulum exhibit two lobes, the lobi inferiores (Plate 24, fig. 46 D, *l.in.*), which are continued posteriorly into the crura cerebri.

The pituitary body† (Plate 24, figs. 44, 45, 46 E, *pt.*) is small, not divided into lobes, and provided with a very minute lumen.

In front of the infundibulum is the optic chiasma (Plate 24, fig. 46 D, *op.ch.*), which is developed very early. It is, as stated by MÜLLER, a true chiasma.

The mid-brain (Plate 24, figs. 44 and 45, *m.b.*) is large, and consists in both stages of (1) a thickened floor forming the crura cerebri, the central canal of which constitutes the iter a tertio ad quartum ventriculum; and (2) the optic lobes (Plate 24, figs. 46 E, F, G, *op.l.*) above, each of which is provided with a cavity continuous with the median iter. The optic lobes are separated dorsally and in front by a well-marked median longitudinal groove. Posteriorly they largely overlap the cerebellum. In the anterior part of the optic lobes, at the point where the iter joins the third ventricle, there may be seen slight projections of the floor into the lumen of the optic lobes (Plate 24, fig. 46 E). These masses probably become in the adult the more conspicuous prominences of the floor of the ventricles of the optic lobes, which we regard as homologous with the tori semicirculares of the brain of the Teleostei.

The hind-brain is formed of the usual divisions, viz.: cerebellum and medulla oblongata (Plate 24, figs. 44 and 45, *cb., md.*). The former constitutes a bilobed projection of the roof of the hind-brain. Only a small portion of it is during these stages left

* Vide F. M. BALFOUR, 'Comparative Embryology,' vol. ii., pp. 355-6, where it is suggested that this commissure is the homologue of the grey commissure of higher types.

† We have not been able to work out the early development of the pituitary body as satisfactorily as we could have wished. In Plate 24, fig. 40, there is shown an invagination of the oral epithelium to form it; in Plate 24, figs. 41 and 42, it is represented in transverse section in two consecutive sections. Anteriorly it is still connected with the oral epithelium (fig. 41), while posteriorly it is free. It is possible that an earlier stage of it is shown in Plate 23, fig. 35. Were it not for the evidence in other types of its being derived from the epiblast we should be inclined to regard it as hypoblastic in origin.

uncovered by the optic lobes, but the major part extends forwards for a considerable distance under the optic lobes, as shown in the transverse sections (Plate 24, figs. 46 F and G, *cb.*); and its two lobes, each with a prolongation of its cavity, are continued forwards beyond the opening of the iter into the fourth ventricle.

It is probable that the anterior horns of the cerebellum are equivalent to the prolongations of the cerebellum into the central cavity of the optic lobes of Teleostei, which are continuous with the so-called fornix of GÖTTSCHE.

III. *Comparison of the larval and adult brain of Lepidosteus, together with some observations on the systematic value of the characters of the Ganoid brain.*

The brain of the older of the two larvæ, which we have described, sufficiently resembles in most of its features that of the adult to render material assistance in the interpretation of certain of the parts of the latter. It will be remembered that in the adult brain the parts usually held to be olfactory lobes were described as the anterior cerebral lobes. The grounds for this will be apparent by a comparison of the cerebrum of the larva and adult. In the larva the cerebrum is formed of (1) an unpaired basal portion with a thin roof, and (2) of a pair of anterior lobes, with small olfactory bulbs at their free extremities.

The basal portion in the larva clearly corresponds in the adult with the basal portion, together with the two posterior cerebral lobes, which are merely special outgrowths of the dorsal edge of the primitive basal portion. The pair of anterior lobes have exactly the same relations in the larva as in the adult, except that in the former the ventricles are prolonged for their whole length instead of being confined to their proximal portions. If, therefore, our identifications of the larval parts of the brain are correct, there can hardly be a question as to our identifications of the parts in the adult. As concerns these identifications, the comparison of the brain of our two larvæ appears conclusive in favour of regarding the anterior lobes as parts of the cerebrum, as distinguished from the olfactory lobes, in that they are clearly derived from the undivided anterior portion of the cerebrum of the younger larva.

The comparison of the larval brain with that of the adult again appears to us to leave no doubt that the vesicle attached to the roof of the thalamencephalon in the adult is the same structure as the bilobed outgrowth of this roof in the larva; and since there is in addition a well-developed pineal gland in the larva with the usual relations, there can be no ground for identifying the vesicle in the adult with the pineal gland.

MÜLLER, in his often quoted memoir (No. 13), states that the brains of Ganoids are peculiar and distinct from those both of Teleostei and Elasmobranchii; but in addition to pointing out that the optic nerves form a chiasma he does not particularly mention the features, to which he alludes in general terms. More recently WILDER (No. 15) has returned to this subject; and though, as we have already had occasion to point out, we cannot accept all his identifications of the parts of the Ganoid brain, yet he

has called attention to certain characteristic features of the cerebrum which have an undoubted systematic value.

The distinctive characters of the Ganoid brain are, in our opinion, (1) the great elongation of the region of the thalamencephalon; and (2) the unpaired condition of the posterior part of the cerebrum, and the presence of so thin a roof to the ventricle of this part as to cause it to appear open above.

The immense length of the region of the thalamencephalon is a feature in the Ganoid brain which must at once strike any one who examines figures of the brains of *Chondrostrei*, *Polypterus*, or *Amia*. It is less striking in the adult *Lepidosteus*, though here also we have shown that the thalamencephalon is really very greatly developed; but in the larva of *Lepidosteus* this feature is still better marked, so that the brain of the larva may be described as being more characteristically Ganoid than that of the adult.

The presence of a largely developed thalamencephalon at once distinguishes a Ganoid brain from that of a Teleostean Fish, in which the optic thalami are very much reduced; but *Lepidosteus* shows its Teleostean affinities by a commencing reduction of this part of the brain.

The large size of the thalamencephalon is also characteristic of the Ganoid brain in comparison with the brain of the Dipnoi; but is not however so very much more marked in the Ganoids than it is in some Elasmobranchii.

On the whole, we may consider the retention of a large thalamencephalon as a primitive character.

The second feature which we have given as characteristic of the Ganoid brain is essentially that which has been insisted upon by WILDER, though somewhat differently expressed by him.

The simplest condition of the cerebrum is that found in the larva of *Lepidosteus*, where there is an anterior pair of lobes, and an undivided posterior portion with a simple prolongation of the third ventricle, and a very thin roof. The dorsal edges of the posterior portion, adjoining the thin roof, usually become somewhat everted (cf. WILDER), and in *Lepidosteus* these edges have in the adult a very great development, and form (vide Plate 25, fig. 47 A-C, *ce'*.) two prominent lobes, which we have spoken of as the posterior cerebral lobes.

These characters of the cerebrum are perhaps even more distinctive than those of the thalamencephalon.

In Teleostei the cerebrum appears to be completely divided into two hemispheres, which are, however, all but solid, the lateral ventricles being only prolonged into their bases. In Dipnoi again there is either (*Protopterus*, WIEDERSHEIM*) a completely separated pair of oval hemispheres, not unlike those of the lower Amphibia, or the oval hemispheres are not completely separated from each other (*Ceratodus*, HUXLEY,†

* 'Morphol. Studien,' iii. Jena, 1880.

† "On *Ceratodus Forsteri*," Proc. Zool. Soc., 1876.

Lepidosiren, HYRTL*); in either case the hemispheres are traversed for the whole length by lateral ventricles which are either completely or nearly completely separated from each other.

In Elasmobranchii the cerebrum is an unpaired though bilobed body, but traversed by two completely separated lateral ventricles, and without a trace of the peculiar membranous roof found in Ganoids.

Not less interesting than the distinguishing characters of the Ganoid brain are those cerebral characters which indicate affinities between *Lepidosteus* and other groups. The most striking of these are, as might have been anticipated, in the direction of the Teleostei.

Although the foremost division of the brain is very dissimilar in the two groups, yet the hind-brain in many Ganoids and the mid-brain also in *Lepidosteus* approaches closely to the Teleostean type. The most essential feature of the cerebellum in Teleostei is its prolongation forwards into the ventricles of the optic vesicles as the valvula cerebelli. We have already seen that there is a homologous part of the cerebellum in *Lepidosteus*; STANNIUS also describes this part in the Sturgeon, but no such part is represented in MÜLLER'S figure of the brain of *Polypterus*, or described by him in the text.

The cerebellum is in most Ganoids relatively smaller, and this is even the case with *Amia*; but the cerebellum of *Lepidosteus* is hardly less bulky than that of most Teleostei.

The presence of tori semicirculares on the floor of the mid-brain of *Lepidosteus* again undoubtedly indicates its affinities with the Teleostei, and such processes are stated by STANNIUS to be absent in the Sturgeon, and have not, so far as we are aware, been described in other Ganoids. Lastly we may point to the presence of well-developed lobi inferiores in the brain of *Lepidosteus* as an undoubted Teleostean character.

On the whole, the brain of *Lepidosteus*, though preserving its true Ganoid characters, approaches more closely to the brain of the Teleostei than that of any other Ganoid, including even *Amia*.

It is not easy to point elsewhere to such marked resemblances of the Ganoid brain, as to the brain of the Teleostei.

The division of the cerebrum into anterior and posterior lobes, which is found in *Lepidosteus*, probably reappears again, as already indicated, in the higher Amphibia. The presence of the peculiar vesicle attached to the roof of the thalamencephalon has its parallel in the brain of *Protopterus*, and as pointing in the same direction a general similarity in the appearance of the brain of *Polypterus* to that of the Dipnoi may be mentioned.

There appears to us to be in no points a close resemblance between the brain of Ganoids and that of Elasmobranchii.

* '*Lepidosiren puruloza*.' Prag., 1845.

SENSE ORGANS.

Olfactory organ.

Development.—The nasal sacs first arise during the late embryonic period in the form of a pair of thickened patches of the nervous layer of the epiblast on the dorsal surface of the front end of the head (Plate 24, fig. 39, *ol.*). The patches very soon become partially invaginated; and a small cavity is developed between them and the epidermic layer of the epiblast (Plate 24, figs. 42 and 43, *ol.*). Subsequently, the roof of this space, formed by the epidermic layer of the epiblast, is either broken through or absorbed; and thus open pits, *lined entirely by the nervous layer of the epidermis*, are formed.

We are not acquainted with any description of an exactly similar mode of origin of the olfactory pits, though the process is almost identical with that of the other sense organs.

We have not worked out in detail the mode of formation of the double openings of the olfactory pits, but there can be but little doubt that it is caused by the division of the single opening into two.

The olfactory nerve is formed very early (Plate 24, fig. 39, I), and, as MARSHALL has found in Aves and Elasmobranchii, it arises at a stage prior to the first differentiation of an olfactory bulb as a special lobe of the brain.

The Eye.

Anatomy.—We have not made a careful histological examination of the eye of *Lepidosteus*, which in our specimens was not sufficiently well preserved for such a purpose; but we have found a vascular membrane enveloping the vitreous humour on its retinal aspect, which, so far as we know, is unlike anything which has so far been met with in the eye of any other adult Vertebrate.

The membrane itself is placed immediately outside the hyaloid membrane, *i.e.*, on side of the hyaloid membrane bounding the vitreous humour. It is easily removed from the retina, to which it is only adherent at the entrance of the optic nerve. In both the eyes we examined it also adhered, at one point, to the capsule of the lens, but we could not make out whether this adhesion was natural, or artificially produced by the coagulation of a thin layer of albuminous matter. In one instance, at any rate, the adhesion appeared firmer than could easily be produced artificially.

The arrangement of the vessels in the membrane is shown diagrammatically in Plate 25, fig. 49, while the characteristic form of the capillary plexus is represented in Plate 25, fig. 50.

The arterial supply appears to be derived from a vessel perforating the retina close to the optic nerve, and obviously homologous with the artery of the processus falci-formis and pecten of Teleostei and Birds, and with the arteria centralis retinæ of Mammals. From this vessel branches diverge and pursue a course towards the

periphery. They give off numerous branches, the blood from which enters a capillary plexus (Plate 25, figs. 49 and 50) and is collected again by veins, which pass outwards and finally bend over and fall into (Plate 25, fig. 49) a circular vein (*cr.v.*) placed at the outer edge of the retina along the insertion of the iris (*ir*). The terminal branches of some of the main arteries appear also to fall directly into this vein.

The membrane supporting the vessels just described is composed of a transparent matrix, in which numerous cells are embedded (Plate 25, fig. 50).

Development.—In the account of the first stages of development of *Lepidosteus*, the mode of formation of the optic cup, the lens, &c., have been described (vide Plates 22 and 23, figs. 23, 26, 35). With reference to the later stages in the development of the eye, the only subject with which we propose to deal is the growth of the mesoblastic processes which enter the cavity of the vitreous humour through the choroid slit.

Lepidosteus is very remarkable for the great number of mesoblast cells which thus enter the cavity of the vitreous humour, and for the fact that these cells are *at first unaccompanied by any vascular structures* (Plate 24, fig. 43, *v.h.*). The mesoblast cells are scattered through the vitreous humour, and there can be no doubt that during early larval life, at a period however when the larva is certainly able to see, every histologist would consider the vitreous humour to be a tissue formed of scattered cells, with a large amount of intercellular substance; and the fact that it is so appears to us to demonstrate that KESSLER's view of the vitreous humour being a mere transudation is not tenable.

In the larva five or six days after hatching, and about 15 millims. in length, the choroid slit is open for its whole length. The edges of the slit near the lens are folded, so as to form a ridge projecting into the cavity of the vitreous humour, while nearer the insertion of the optic nerve they cease to exhibit any such structure. The mesoblast, though it projects between the lips of the ridge near the lens, only extends through the choroid slit into the cavity of the vitreous humour in the neighbourhood of the optic nerve. Here it forms a lamina with a thickened edge, from which scattered cells in the cavity of the vitreous humour seem to radiate.

At a slightly later stage than that just described, blood-vessels become developed within the cavity of the vitreous humour, and form the vascular membrane already described in the adult, placed close to the layer of nerve-fibres of the retina, but separated from this layer by the hyaloid membrane (Plate 25, fig. 48, *v.sh.*). The artery bringing the blood to the above vascular membrane is bound up in the same sheath as the optic nerve, and passes through the choroid slit very close to the optic nerve. Its entrance into the cavity of the vitreous humour is shown in Plate 25, fig. 48 (*vs.*); its relation to the optic nerve in Plate 24, fig. 46, C and D (*vs.*).

The above sheath has, so far as we know, its nearest analogue in the eye of *Alytes*, where, however, it is only found in the larva.

The reader who will take the trouble to refer to the account of the imperfectly-developed processus falciformis of the Elasmobranch eye in the treatise 'On Comparative

Embryology,' by one of us,* will not fail to recognise that the folds of the retina at the sides of the choroid slit, and the mesoblastic process passing through this slit, are strikingly similar in *Lepidosteus* and *Elasmobranchii*; and that, if we are justified in holding them to be an imperfectly-developed *processus falciformis* in the one case, we are equally so in the other.

JOHANNES MÜLLER mentions the absence of a *processus falciformis* as one of the features distinguishing Ganoids and Teleostei. So far as the systematic separation of the two groups is concerned, he is probably perfectly justified in this course; but it is interesting to notice that both in Ganoids and *Elasmobranchii* we have traces of a structure which undergoes a very special development in the Teleostei, and that the *processus falciformis* of Teleostei is therefore to be regarded, not as an organ peculiar to them, but as the peculiar modification within the group of a primitive Vertebrate organ.

SUCTORIAL DISC.

One of the most remarkable organs of the larval *Lepidosteus* is the suctorial disc, placed at the front end of the head, to which we have made numerous allusions in the first section of this memoir.

The external features of the disc have been fully dealt with by AGASSIZ, and he also explained its function by observations on the habits of the larva. We have already quoted (p. 371) a passage from AGASSIZ' memoir showing how the young Fishes use the disc to attach themselves firmly to any convenient object. The discs appear in fact to be highly efficient organs of attachment, in that the young Fish can remain suspended by them to the sides of the jar, even after the water has been lowered below the level at which they are attached.

The disc is formed two or three days before hatching, and from AGASSIZ' statements, it appears to come into use immediately the young Fish is liberated from the egg membranes.

We have examined the histological structure of the disc at various ages of its growth, and may refer the reader to Plate 21, figs. 11 and 13, and Plate 24, figs. 40 and 44. The result of our examination has been to show that the disc is provided with a series of papillæ often exhibiting a bilateral arrangement. The papillæ are mainly constituted of highly modified cells of the mucous layer of the epidermis. These cells have the form of elongated columns, the nucleus being placed at the base, and the main mass of the cells being filled with a protoplasmic reticulum. They may probably be regarded as modified mucous cells. In the mesoblast adjoining the suctorial disc there are numerous sinus-like vascular channels.

It does not appear probable that the disc has a true sucking action. It is unprovided with muscular elements, and there appears to be no mechanism by which it could act as a sucking organ. We must suppose, therefore, that its adhesive power depends upon the capacity of the cells composing its papillæ to pour out a sticky secretion.

* Vol. ii., p. 414.

MUSCULAR SYSTEM.

There is a peculiarity in the muscular system of *Lepidosteus*, which so far as we know has not been previously noticed. It is that the lateral muscles of each side are not divided, either in the region of the trunk or of the tail, into a dorso-lateral and ventro-lateral division.

This peculiarity is equally characteristic of the older larvæ as of the adult, and is shown in Plate 28, figs. 67, 72, and 73, and Plate 29, figs. 74–76. In the Cyclostomata the lateral muscles are not divided into dorsal and ventral sections; but except in this group such a division has been hitherto considered as invariable amongst Fishes.

This character must, without doubt, be held to be the indication of a very primitive arrangement of the muscular system. In the embryos of all Fishes with the usual type of the lateral muscles, the undivided condition of the muscles precedes the divided condition; and in primitive forms such as the Cyclostomata and Amphioxus the embryonic condition is retained, as it is in *Lepidosteus*.

SKELETON.

Part I.—*Vertebral column and ribs of the adult.*

A typical vertebra from the trunk of *Lepidosteus* has the following characters (Plate 29, figs. 80 and 81).

The centrum is slightly narrower in the middle than at its two extremities. It articulates with adjacent vertebræ by a convex face in front and a concave face behind, being thus, according to OWEN'S nomenclature, opisthocœlous. It presents on its under surface a well-marked longitudinal ridge, which in many vertebræ is only united at its two extremities with the main body of the vertebra.

From the lateral borders of the centrum there project, at a point slightly nearer the front than the hind end, a pair of prominent hæmal processes (*h.a.*), to the ends of which are articulated the ribs. These processes have a nearly horizontal direction in the greater part of the trunk, though bent downwards in the tail.

The neural arches (*n.a.*) have a somewhat complicated form. They are mainly composed of two vertical plates, the breadth of the basal parts of which is nearly as great as the length of the vertebræ, so that comparatively narrow spaces are left between the neural arches of successive vertebræ for the passage of the spinal nerves. Some little way from its dorsal extremity each neural arch sends a horizontal process inwards, which meets its fellow and so forms a roof for the spinal canal. These processes appear to be confined to the posterior parts of the vertebræ, so that at the front ends of the vertebræ, and in the spaces between them, the neural canal is without an osseous roof. Above the level of this osseous roof there is a narrow passage, bounded laterally by the dorsal extremities of the neural plates. This passage is mainly filled up by a series of cartilaginous elements (Plate 29, figs. 80 and 81, *i.c.*) (probably

fibro-cartilage), which rest upon the roof of the neural canal. Each element is situated *intervertebrally*, its anterior end being wedged in between the two dorsal processes of the neural arch of the vertebra in front, and its posterior end extending for some distance over the vertebra behind. The successive elements are connected by fibrous tissue, and are continuous dorsally with a fibrous band, known as the ligamentum longitudinale superius (Plate 29, figs. 80 and 81, *l.l.*), characteristic of Fishes generally, and running continuously for the whole length of the vertebral column. Each of the cartilaginous elements is, as will be afterwards shown, developed as two independent pieces of cartilage, and might be compared with the dorsal element which usually forms the keystone of the neural arch in Elasmobranchs, were not the latter vertebral instead of intervertebral in position. More or less similar elements are described by GÖTTE in the neural arches of many Teleostei, which also, however, appear to be vertebrally placed, and he has compared them and the corresponding elements in the Sturgeon with the Elasmobranch cartilages forming the keystone of the neural arch. GÖTTE does not, however, appear to have distinguished between the cartilaginous elements, and the osseous elements forming the roof of the spinal canal, which are true membrane bones; it is probable that the two are not so clearly separated in other types as in *Lepidosteus*.

The posterior ends of the neural plates of the neural arches are continued into the dorsal processes directed obliquely upwards and backwards, which have been somewhat unfortunately described by STANNIUS as rib-like projections of the neural arch. The dorsal processes of the two sides do not meet, but between them is placed a median free spinous element, also directed obliquely upwards and backwards, which forms a kind of roof for the groove in which the cartilaginous elements and the ligamentum longitudinale are placed.

The vertebræ are wholly formed of a very cellular osseous tissue, in which a distinction between the bases of the neural and hæmal processes and the remainder of the vertebra is not recognisable. The bodies of the vertebræ are, moreover, directly continuous with the neural and hæmal arches.

The ribs in the region of the trunk are articulated to the ends of the long hæmal processes. They envelop the body cavity, their proximal parts being placed immediately outside the peritoneal membrane, along the bases of the intermuscular septa. Their distal ends do not, however, remain close to the peritoneal membrane, *but pass outwards along the intermuscular septa till their free ends come into very close proximity with the skin*. This peculiarity, which holds good in the adult for all the free ribs, is shown in one of the anterior ribs of an advanced larva in Plate 28, fig. 72 (*rb.*). We are not aware that this has been previously noticed, but it appears to us to be a point not without interest in all questions which concern the homology of rib-like structures occupying different positions in relation to the muscles. Its bearings are fully dealt with in the section of this paper devoted to the consideration of the homologies of the ribs in Fishes.

As regards the behaviour of the ribs in the transitional region between the trunk and the tail, we cannot do better than translate the description given by GEGENBAUR of this region (No. 6, p. 411):—"Up to the 34th vertebra the ribs borne by the laterally and posteriorly directed processes present nothing remarkable, though they have gradually become shorter. The ribs of the 35th vertebra exhibit a slight curvature outwards of their free ends, a peculiarity still more marked in the 36th. The last named pair of ribs converge somewhat in their descent backwards so that both ribs decidedly approach before bending outwards. The 37th vertebra is no longer provided with freely terminating ribs, but on the contrary, the same pair of processes which in front was provided with ribs, bears a short forked process as the hæmal arch. *The two, up to this point separated ribs, have here formed a hæmal arch by the fusion of their lower ends, which arch is movable just like the ribs, and, like them, is attached to the vertebral column.*"

In the region of the tail fin the hæmal arches supporting the caudal fin rays are very much enlarged.

Part II.—*Development of the vertebral column and ribs.*

The first development and early histological changes of the notochord have already been given, and we may take up the history of the vertebral column at a period when the notochord forms a large circular rod, whose cells are already highly vacuolated, while the septa between the vacuoles form a delicate wide-meshed reticulum. Surrounding the notochord is the usual cuticular sheath, which is still thin.

The first indications of the future vertebral column are to be found in the formation of a distinct mesoblastic investment of the notochord. On the dorsal aspect of the notochord, the mesoblast forms two ridges, one on each side, which are prolonged upwards so as to meet above the neural canal, for which they form a kind of sheath. On the ventral side of the notochord there are also two ridges, which are, however, except on the tail, much less prominent than the dorsal ridges.

The changes which next ensue are practically identical with those which take place in Teleostei. Around the cuticular sheath of the notochord there is formed an elastic membrane—the *membrana elastica externa*. At the same time the basal parts of the dorsal, or as we may perhaps more conveniently call them, the neural ridges of the notochord become enlarged at each intermuscular septum, and the tissue of these enlargements soon becomes converted into cartilage, thus forming a series of independent paired neural processes riding on the *membrana elastica externa* surrounding the notochord, and extending about two-thirds of the way up the sides of the medullary cord. They are shown in transverse section in Plate 28, fig. 67 (*n.a.*), and in a side view in fig. 68 (*n.a.*).

Simultaneously with the neural arches, the hæmal arches also become established, and arise by the formation of similar enlargements of the ventral or hæmal ridges. In the trunk they are very small, but in the region of the tail their condition is very

different. At the front end of the anal fin the paired hæmal arches suddenly enlarge and extend ventralwards (Plate 28, fig. 67, *h.a.*).

Each succeeding pair of arches becomes larger than the one in front, and the two elements of each arch first nearly meet below the caudal vein (Plate 28, fig. 67) and finally actually do so, forming in this way a completely closed hæmal canal. At the point where they first meet the permanent caudal fin commences, and here (Plate 28, fig. 68) we find that not only do the hæmal arches meet and coalesce below the caudal vein, but they are actually produced into long spines supporting the fin rays of the caudal fin, which thus differs from the other fins in being supported by parts of the true vertebral column and not by independently formed elements of the skeleton.

Each of the large caudal hæmal arches, including the spine, forms a continuous whole, and arises at an earlier period of larval life than any other part of the vertebral column. We noticed the first indications of the neural arches in the larva of about a week old, while they are converted into fully formed cartilage in the larva of three weeks.

The neural and hæmal arches, resting on the *membrana elastica externa*, do not at this early stage in the least constrict the notochord. They grow gradually more definite, till the larva is five or six weeks old and about 26 millims. in length, but otherwise for a long time undergo no important changes. During the same period, however, the true sheath of the notochord greatly increases in thickness, and the *membrana elastica externa* becomes more definite. So far it would be impossible to distinguish the development of the vertebral column of *Lepidosteus* from that of a Teleostean Fish.

Of the stages immediately following we have unfortunately had no examples, but we have been fortunate enough to obtain some young specimens of *Lepidosteus*,* which have enabled us to work out with tolerable completeness the remainder of the developmental history of the vertebral column. In the next oldest larva, of about 5.5 centims., the changes which have taken place are already sufficient to differentiate the vertebral column of *Lepidosteus* from that of a Teleostean, and to show how certain of the characteristic features of the adult take their origin.

In the notochord the most important and striking change consists in the appearance of a series of very well marked vertebral constrictions *opposite the insertions of the neural and hæmal arches*. The first constrictions of the notochord are thus, as in other Fishes, vertebral; and although, owing to the growth of the intervertebral cartilage, the vertebral constrictions are subsequently replaced by intervertebral constrictions, yet at the same time the primitive occurrence of vertebral constrictions demonstrates that the vertebral column of *Lepidosteus* is a modification of a type of vertebral column with biconcave vertebrae.

The structure of the gelatinous body of the notochord has undergone no important change. The sheath, however, exhibits certain features which deserve careful descrip-

* These specimens were given to us by Professor W. K. PARKER, who received them from Professor BURT G. WILDER.

tion. In the first place the attention of the observer is at once struck by the fact that, in the vertebral regions, the sheath is much thicker (.014 millim.) than in the intervertebral (.005 millim.), and a careful examination of the sheath in longitudinal sections shows that the thickening is due to the special differentiation of a superficial part (Plate 28, fig. 69, *sh.*) of the sheath in each vertebral region. This part is somewhat granular as compared to the remainder, especially in longitudinal sections. It forms a cylinder (the wall of which is about .01 millim. thick) in each vertebral region, immediately within the membrana elastica externa. Between it and the gelatinous tissue of the notochord within there is a very thin unmodified portion of the sheath, which is continuous with the thinner intervertebral parts of the sheath. This part of the sheath is faintly, but at the same time distinctly, concentrically striated—a probable indication of concentric fibres. The inner unmodified layer of the sheath has the appearance in transverse sections through the vertebral regions of an inner membrane, and may perhaps be KÖLLIKER'S "membrana elastica interna."

We are not aware that any similar modification of the sheath has been described in other forms.

The whole sheath is still invested by a very distinct membrana elastica externa (*m.el.*).

The changes which have taken place in the parts which form the permanent vertebræ will be best understood from Plate 28, figs. 69–71. From the transverse section (fig. 70) it will be seen that there are still neural and hæmal arches resting upon the membrana elastica externa; but longitudinal sections (fig. 69) show that laterally these arches join a cartilaginous tube, embracing the intervertebral regions of the notochord, and continuous from one vertebra to the next.

It will be convenient to treat separately the neural arches, the hæmal arches with their appendages, and the intervertebral cartilaginous rings.

The neural arches, except in the fact of embracing a relatively smaller part of the neural tube than in the earlier stage, do not at first sight appear to have undergone any changes. Viewed from the side, however, in dissected specimens, they are seen to be prolonged upwards so as to unite above with bars of cartilage directed obliquely backwards. An explanation of this appearance is easily found in the sections. The cartilaginous neural arches are invested by a delicate layer of homogeneous bone, developed in the perichondrium, and this bone is prolonged beyond the cartilage and joins a similar osseous investment of the dorsal bars above mentioned. The whole of these parts may, it appears to us, be certainly reckoned as parts of the neural arches, so that at this stage each neural arch consists of: (1) a pair of basal portions resting on the notochord consisting of cartilage invested by bone, (2) of a pair of dorsal cartilaginous bars invested in bone (*n.a'*), and (3) of osseous bars connecting (1) and (2).

Though, in the absence of the immediately preceding stages, it is not perfectly certain that the dorsal pieces of cartilage are developed independently of the ventral, there appears to us every probability that this is so; and thus the cartilage of each neural arch is developed discontinuously, while the permanent bony neural arch,

which commences as a deposit of bone partly in the perichondrium and partly in the intervening membrane, forms a continuous structure.

Analogous occurrences have been described by GÖTTE in Teleostei.

The dorsal portion of each neural arch becomes what we have called the dorsal process of the adult arch.

Between the dorsal processes of the two sides there is placed a median rod of cartilage (Plate 28, fig. 70, *i.s.*), which in its development is wholly independent of the true neural arches, and which constitutes the median spinous element of the adult. In tracing these backwards it becomes obvious that they are homologous with the interspinous elements supporting the dorsal fin, in that they are replaced by these interspinous elements in the region of the dorsal fin, and that the interspinous bones occupy the same position as the median spinous processes. This homology was first pointed out by GÖTTE in the case of the Teleostei.

Immediately beneath this rod is placed the longitudinal ligament (Plate 28, fig. 70, *l.l.*), but there is as yet no trace of a junction between the neural arches of the two sides in the space between the longitudinal ligament and the spinal cord.

The basal parts of the neural arches of the two sides are united dorsally by a thin cartilaginous layer resting on the sheath of the notochord, but they are not united ventrally with the hæmal arches.

The hæmal processes in the trunk are much more prominent than in the preceding stage, and their bases are united ventrally by a tolerably thick layer of cartilage. In the trunk they are continuous with the so-called ribs of the adult (Plate 28, fig. 70); but in order to study the nature of these ribs it is necessary to trace the modifications undergone by the hæmal arches in passing from the tail to the trunk.

It will be remembered that at an earlier stage the hæmal arches in the region of the tail-fin were fully formed, and that through the anterior part of the caudal region the hæmal processes were far advanced in development, and just in front of the caudal fin had actually met below the caudal vein.

The mode of development of the hæmal arches in the tail as *unjointed* cartilaginous bars investing the caudal arteries and veins is so similar to that of the caudal hæmal arches of Elasmobranchii, that it appears to us impossible to doubt their identity in the two groups.*

* GEGENBAUR (No. 6) takes a different view on this subject, as is clear from the following passage in this memoir (pp. 369-370):—"Each vertebra of *Lepidosteus* thus consists of a section of the notochord, and of the cartilaginous tissue surrounding its sheath, which gives origin to the upper arches for the whole length of the vertebral column, and in the caudal region to that of the lower arches also. *The latter do not however complete the enclosure of a lower canal, but this is effected by special independent elements, which are to be interpreted as homologues of the ribs.*" (The italics are ours.) While we fully accept the homology between the ribs and the lower elements of the hæmal arches of the tail, the view expressed in the italicised section, to the effect that the lower parts of the caudal arches are not true hæmal arches but are independently formed elements, is entirely opposed to our observations, and has we

The changes which have taken place by this stage with reference to the hæmal arches of the tail are not very considerable.

In the case of a few more vertebræ the hæmal processes have united into an arch, and the spinous processes of the arches in the region of the caudal fin have grown considerably in length. A more important change is perhaps the commencement of a segmentation of the distal parts of the hæmal arches from the proximal. This process has not, however, as yet resulted in a complete separation of the two, such as we find in the adult.

If the hæmal processes are traced forwards (Plate 29, figs. 75 and 76) from the anterior segment where they meet ventrally, it will be found that each hæmal process consists of a basal portion, adjoining the notochord, and a peripheral portion. These two parts are completely continuous, but the line of a future separation is indicated by the structure of the cartilage, though not shown in our figures. As the true body cavity of the trunk replaces the obliterated body cavity of the caudal region, no break of continuity will be found in the structure of the hæmal processes (Plates 28 and 29, figs. 73 and 74), but while the basal portions grow somewhat larger, the peripheral portions gradually elongate and take the form of delicate rods of cartilage extending ventralwards, on each side of the body cavity, immediately outside the peritoneal membrane, and along the lines of insertion of the intermuscular septa. These rods obviously become the ribs of the adult.

As one travels forwards the ribs become continually longer and more important, and though they are at this stage united with the hæmal processes in every part of the trunk, yet they are much more completely separated from these processes in front than behind (Plate 28, fig. 72).

In front (Plate 28, fig. 72), each rib (*rb.*), after continuing its ventral course for some distance, immediately outside the peritoneal membrane, turns outwards, and passes along one of the intermuscular septa till it reaches the epidermis. This feature in the position of the ribs is, as has been already pointed out in the anatomical part of this section, characteristic of all the ribs of the adult.

It is unfortunate that we have had no specimens showing the ribs at an earlier stage of development; but it appears hardly open to doubt that *the ribs are originally continuous with the hæmal processes*, and that the indications of a separation between those two parts at this stage are not due to a secondary fusion, but to a commencing segmentation.

It further appears, as MÜLLER, GEGENBAUR and others have stated, that the ribs and hæmal processes of the tail are serially homologous structures; but that the view maintained by GÖTTE in his very valuable memoirs on the Vertebrate skeleton is also correct to the effect that *the hæmal arches of the tail are homologous throughout the series of Fishes*.

believe only arisen from the fact that GEGENBAUR had not the young larvæ to work with by which alone this question could be settled

To this subject we shall return again at the end of the section.

Before leaving the hæmal arches it may be mentioned that behind the region of the ventral caudal fin the two hæmal processes merge into one, and form an unpaired knob resting on the ventral side of the notochord, and not perforated by a canal.

There are now present well-developed intervertebral rings of cartilage, each of which eventually becomes divided into two parts, and converted into the adjacent faces of the contiguous vertebræ. These rings are united with the neural and hæmal arches of the vertebræ in front and behind.

Each ring, as shown by the transverse section (Plate 28, fig. 71), is not uniformly thick, but exhibits four projections, two dorsal and two ventral. These four projections are continuous with the bases of the neural and hæmal arches of the adjacent vertebræ, and afford presumptive evidence of the derivation of the intervertebral rings from the neural and hæmal arches; in that had they so originated, it would be natural to anticipate the presence of four thickenings indicating the four points from which the cartilage had spread, while if the rings had originated independently, it would not be easy to give any explanation of the presence of such thickenings. GEGENBAUR (No. 6), from the investigation of a much older larva than that we are now describing, also arrived at the conclusion that the intervertebral cartilages were derived from the neural and hæmal arches; but as doubts have been thrown upon this conclusion by GÖTTE, and as it obviously required further confirmation, we have considered it important to attempt to settle this point. From the description given above, it is clear that we have not, however, been able absolutely to trace the origin of this cartilage, but at the same time we think that we have adduced weighty evidence in corroboration of GEGENBAUR'S view.

As shown in longitudinal section (Plate 28, fig. 69, *iv.r.*), the intervertebral rings are thicker in the middle than at the two ends. In this thickened middle part the division of the cartilage into two parts to form the ends of two contiguous vertebræ is subsequently effected. The curved line which this segmentation will follow is, however, already marked out, and from surface views it might be supposed that this division had actually occurred.

The histological structure of the intervertebral cartilage is very distinct from that of the cartilage of the bases of the arches, the nuclei being much more closely packed. In parts, indeed, the intervertebral cartilage has almost the character of fibro-cartilage. On each side of the line of division separating two vertebræ it is invested by a superficial osseous deposit.

The next oldest larva we have had was 11 centims. in length. The filamentous dorsal lobe of the caudal fin still projected far beyond the permanent caudal fin (Plate 21, fig. 16).

The vertebral column was considerably less advanced in development than that dissected by GEGENBAUR, though it shows a great advance on the previous stage. Its features are illustrated by two transverse sections, one through the median plane of a

vertebral region (Plate 29, fig. 78) and the other through that of an intervertebral region (Plate 29, fig. 79), and by a horizontal section (Plate 29, fig. 77).

In the last stage the notochord was only constricted vertebally. Now, however, by the great growth of intervertebral cartilage there have appeared (Plate 29, fig. 77) very well-marked *intervertebral* constrictions, by the completion of which the vertebræ of *Lepidosteus* acquire their unique character amongst Fishes.

These constrictions still, however, coexist with the earlier, though at this stage relatively less conspicuous, vertebral constrictions.

The gelatinous body of the notochord retains its earlier condition. The sheath has, however, undergone some changes. In the vertebral regions there is present in any section of the sheath—(1) externally, the membrana elastica externa (*m.el.*); then (2) the external layer of the sheath (*sh.*), which is, however, less thick than before, and exhibits a very faint form of radial striation; and (3) internally, a fairly thick and concentrically striated layer. The whole thickness is, on an average, 0.18 millim.

In the intervertebral regions the membrana elastica externa is still present in most parts, but has become absorbed at the posterior border of each vertebra, as shown in longitudinal section in Plate 29, fig. 77. It is considerably puckered transversely. The sheath of the notochord within the membrana elastica externa is formed of a concentrically striated layer, continuous with the innermost layer of the sheath in the vertebral regions. It is puckered longitudinally. Thus, curiously enough, the membrana elastica externa and the sheath of the notochord in the intervertebral regions are folded in different directions, the folds of the one being only visible in transverse sections (Plate 29, fig. 79), and those of the other in longitudinal sections (Plate 29, fig. 77).

The osseous and cartilaginous structures investing the notochord may conveniently be dealt with in the same order as before, viz.: the neural arches, the hæmal arches, and the intervertebral cartilages.

The cartilaginous portions of the neural arches are still unossified, and form (Plate 29, fig. 78, *n.a.*) small wedge-shaped masses resting on the sheath of the notochord. They are invested by a thick layer of bone prolonged upwards to meet the dorsal processes (*n.a'*), which are still formed of cartilage invested by bone.

It will be remembered that in the last stage there was no key-stone closing in the neural arch above. This deficiency is now however supplied, and consists of (1) two bars of cartilage repeated for each vertebra, but intervertebrally placed, which are directly differentiated from the ligamentum longitudinale superius, into which they merge above; and (2) two osseous plates placed on the outer sides of these cartilages, which are continuous with the lateral osseous bars of the neural arch. The former of these elements gives rise to the cartilaginous elements above the osseous bridge of the neural arch in the adult. The two osseous plates supporting these cartilages clearly form what we have called in our description of the adult the osseous roof of the spinal canal.

A comparison of the neural arch at this stage with the arch in the adult, and in the stage last described, shows that the greater part of the neural arch of the adult is formed of membrane-bone, there being preformed in cartilage only a small basal part, a dorsal process, and paired key-stones below the ligamentum longitudinale superius.

The hæmal arches (Plate 29, fig. 78) are still largely cartilaginous, and rest upon the sheath of the notochord. They are invested by a thick layer of bone. The bony layer investing the neural and hæmal arches is prolonged to form a continuous investment round the vertebral portions of the notochord (Plate 29, fig. 78). This investment is at the sides prolonged outwards into irregular processes (Plate 29, fig. 78), which form the commencement of the outer part of the thick but cellular osseous cylinder forming the middle part of the vertebral body.

The intervertebral cartilages are much larger than in the earlier stage (Plate 29, figs. 77 and 79), and it is by their growth that the intervertebral constrictions of the notochord are produced. They have ceased to be continuous with the cartilage of the arches, the intervening portion of the vertebral body between the two being only formed of bone. They are not yet divided into two masses to form the contiguous ends of adjacent vertebræ.

Externally, the part of each cartilage which will form the hinder end of a vertebral body is covered by a tube of bone, having the form of a truncated funnel, shown in longitudinal section in Plate 29, fig. 77, and in transverse section in Plate 29, fig. 79.

At each end, the intervertebral cartilages are becoming penetrated and replaced by beautiful branched processes from the homogeneous bone which was first of all formed in the perichondrium (Plate 29, fig. 77).

This constitutes the latest stage which we have had.

GEGENBAUR (No. 6) has described the vertebral column in a somewhat older larva of 18 centims.

The chief points in which the vertebral column of this larva differed from ours are: (1) the disappearance of all trace of the primitive vertebral constriction of the notochord; (2) the nearly completed constriction of the notochord in the intervertebral regions; (3) the complete ossification of the vertebral portions of the bodies of the vertebræ, the terminal so-called intervertebral portions alone remaining cartilaginous; (4) the complete ossification of the basal portions of the hæmal and neural processes included within the bodies of the vertebræ, so that in the case of the neural arch all trace of the fact that the greater part was originally not formed in cartilage had become lost. The cartilage of the dorsal spinous processes was, however, still persistent.

The only points which remain obscure in the later history of the vertebral column are the history of the notochord and of its sheath. We do not know how far these are either simply absorbed or partially or wholly ossified.

GÖTTE in his memoir on the formation of the vertebral bodies of the Teleostei

attempts to prove (1) that the so-called *membrana elastica externa* of the Teleostei is not a homogeneous elastica, but is formed of cells, and (2) that in the vertebral regions ossification first occurs in it.

In *Lepidosteus* we have met with no indication that the *membrana elastica externa* is composed of cells; though it is fair to GÖTTE to state that we have not examined such isolated portions of it as he states are necessary in order to make out its structure. But further than this we have satisfied ourselves that during the earlier stage of ossification this membrane is not ossified, and indeed in part becomes absorbed in proximity to the intervertebral cartilages; and GEGENBAUR met with no ossification of this membrane in the later stage described by him.

Summary of the development of the vertebral column and ribs.

A mesoblastic investment is early formed round the notochord, which is produced into two dorsal and two ventral ridges, the former uniting above the neural canal. Around the cuticular sheath of the notochord an elastic membrane, the *membrana elastica externa*, is next developed. The neural ridges become enlarged at each intermuscular septum, and these enlargements soon become converted into cartilage, thus forming a series of neural processes riding on the *membrana elastica externa*, and extending about two-thirds of the way up the sides of the neural canal. The hæmal processes arise simultaneously with, and in the same manner as, the neural. They are small in the trunk, but at the front end of the anal fin they suddenly enlarge and extend ventralwards. Each succeeding pair of hæmal arches becomes larger than the one in front, each arch finally meeting its fellow below the caudal vein, thus forming a completely closed hæmal canal. These arches are moreover produced into long spines supporting the fin-rays of the caudal fin, which thus differs from the other impaired fins in being supported by parts of the vertebral column, and not by separately formed skeletal elements.

In the next stage which we have had the opportunity of studying (larva of $5\frac{1}{2}$ centims.), a series of very well-marked *vertebral* constrictions are to be seen in the notochord. The sheath is now much thicker in the vertebral than in the intervertebral regions: this is due to a special differentiation of a superficial part of the sheath, which appears more granular than the remainder. This granular part of the sheath thus forms a cylinder in each vertebral region. Between it and the gelatinous tissue of the notochord there remains a thin unmodified portion of the sheath, which is continuous with the intervertebral parts of the sheath. The neural and hæmal arches are seen to be continuous with a cartilaginous tube embracing the intervertebral regions of the notochord, and continuous from one vertebra to the next. A delicate layer of bone, developed in the perichondrium, invests the cartilaginous neural arches, and this bone grows upwards so as to unite above with the osseous investment of separately developed bars of cartilage, which are directed obliquely backwards. These bars, or

dorsal processes, may be reckoned as parts of the neural arches. Between the dorsal processes of the two sides is placed a median rod of cartilage, which is developed separately from the true neural arches, and which constitutes the median spinous element of the adult. Immediately below this rod is placed the *ligamentum longitudinale superius*. There is now a commencement of separation between the dorsal and ventral parts of the hæmal arches, not only in the tail, but also in the trunk, where they pass ventralwards on each side of the body cavity, immediately outside the peritoneal membrane, along the lines of insertion of the intermuscular septa. These are obviously the ribs of the adult, and there is no break of continuity of structure between the hæmal processes of the tail and the ribs. In the anterior part of the trunk the ribs pass outwards along the intermuscular septa till they reach the epidermis. Thus the ribs are originally continuous with the hæmal processes. Behind the region of the ventral caudal fin the two hæmal processes merge into one, which is not perforated by a canal.

Each of the intervertebral rings of cartilage becomes eventually divided into two parts, and converted into the adjacent faces of contiguous vertebræ, the curved line where this will be effected being plainly marked out. These rings are united with the neural and hæmal arches of the vertebræ next in front and behind. As these rings are formed originally by the spreading of the cartilage from the primitive neural and hæmal processes, the intervertebral cartilages are clearly derived from the neural and hæmal arches. The intervertebral cartilages are thicker in the middle than at their two ends.

In our latest stage (11 centims.), the vertebral constrictions of the notochord are rendered much less conspicuous by the growth of the intervertebral cartilages giving rise to marked intervertebral constrictions. In the intervertebral regions the *membrana elastica externa* has become aborted at the posterior border of each vertebra, and the remaining part is considerably puckered transversely. The inner sheath of the notochord is puckered longitudinally in the intervertebral regions. The granular external layer of the sheath in the vertebral regions is less thick than in the last stage, and exhibits faint radial striations.

Two closely approximated cartilaginous elements now form a keystone to the neural arch above: these are directly differentiated from the *ligamentum longitudinale superius*, into which they merge above. An osseous plate is formed on the outer side of each of these cartilages. These plates are continuous with the lateral osseous bars of the neural arches, and also give rise to the osseous roof of the spinal canal of the adult.

Thus the greater part of the neural arches is formed of membrane bone. The hæmal arches are invested by a thick layer of bone, and there is also a continuous osseous investment round the vertebral portions of the notochord. The intervertebral cartilages become penetrated by branched processes of bone.

Comparison of the vertebral column of Lepidosteus with that of other forms.

The peculiar form of the articulatory faces of the vertebræ of *Lepidosteus* caused L. AGASSIZ (No. 2) to compare them with the vertebræ of Reptiles, and subsequent anatomists have suggested that they more nearly resemble the vertebræ of some Urodelous Amphibia than those of any other form.

If, however, GÖTTE's account of the formation of the amphibian vertebræ is correct, there are serious objections to a comparison between the vertebræ of *Lepidosteus* and Amphibia on developmental grounds. The essential point of similarity supposed to exist between them consists in the fact that in both there is a great development of intervertebral cartilage which constricts the notochord intervertebrally, and forms the articular faces of contiguous vertebræ.

In *Lepidosteus* this cartilage is, as we have seen, derived from the bases of the arches; but in Amphibia it is held by GÖTTE to be formed by a special thickening of a cellular sheath round the notochord which is probably homologous with the cartilaginous sheath of the notochord of Elasmobranchii, and therefore with part of the notochordal sheath placed within the membrana elastica externa.

If the above statements with reference to the origin of the intervertebral cartilage in the two types are true, it is clear that no homology can exist between structures so differently developed. Provisionally, therefore, we must look elsewhere than in *Lepidosteus* for the origin of the amphibian type of vertebræ.

The researches which we have recorded demonstrate, however, in a very conclusive manner that the vertebræ of *Lepidosteus* have very close affinities with those of Teleostei.

In support of this statement we may point: (1) To the structure of the sheath of the notochord; (2) to the formation of the greater part of the bodies of the vertebræ from ossification in membrane around the notochord; (3) to the early biconcave form of the vertebræ, only masked at a later period by the development of intervertebral cartilages; (4) to the character of the neural arches.

This latter feature will be made very clear if the reader will compare our figures of the sections of later vertebræ (Plate 29, fig. 78) with GÖTTE's* figure of the section of the vertebra of a Pike (plate 7, fig. 1). In GÖTTE's figure there are shown similar intercalated pieces of cartilage to those which we have found, and similar cartilaginous dorsal processes of the vertebræ. Thus we are justified in holding that whether or no the opisthocœlous form of the vertebræ of *Lepidosteus* is a commencement of a type of vertebræ inherited by the higher forms, yet in any case the vertebræ are essentially built on the type which has become inherited by the Teleostei from the bony Ganoids.

* "Beiträge zur vergl. Morphol. d. Skeletsystems d. Wirbeltheire." Archiv. f. Mikr. Anat., vol. xvi., 1879.

Part III.—*The ribs of Fishes.*

The nature and homologies of the ribs of Fishes have long been a matter of controversy; but the subject has recently been brought forward in the important memoirs of GÖTTE* on the Vertebrate skeleton. The alternatives usually adopted are, roughly speaking, these:—Either the hæmal arches of the tail are homologous throughout the piscine series, while the ribs of Ganoids and Teleostei are not homologous with those of Elasmobranchii; or the ribs are homologous in all the piscine groups, and the hæmal arches in the tail are differently formed in the different types. GÖTTE has brought forward a great body of evidence in favour of the first view; while GEGENBAUR† may be regarded as more especially the champion of the second view.

One of us held in a recent publication‡ that the question was not yet settled, though the view that the ribs are homologous throughout the series was provisionally accepted.

It is admitted by both GEGENBAUR and GÖTTE that in *Lepidosteus* the ribs, in the transition from the trunk to the tail, bend inwards, and finally unite in the region of the tail to form the ventral parts of the hæmal arches, and our researches have abundantly confirmed this conclusion.

Are the hæmal arches, the ventral parts of which are thus formed by the coalescence of the ribs, homologous with the hæmal arches in Elasmobranchii? The researches recorded in the preceding pages appear to us to demonstrate in a conclusive manner that they are so.

The development of the hæmal arches in the tail in these two groups is practically identical; they are formed in both as simple elongations of the primitive hæmal processes, which meet below the caudal vein. In the adult there is an apparent difference between them, arising from the fact that in *Lepidosteus* the peripheral parts of the hæmal processes are only articulated with the basal portions, and not, as in Elasmobranchii, continuous with them. This difference does not, however, exist in the early larva, since in the larval *Lepidosteus* the hæmal arches of the tail are unsegmented cartilaginous arches, as they permanently are in Elasmobranchii. If, however, the homology between the hæmal arches of the two types should still be doubted, the fact that in both types the hæmal arches are similarly modified to support the fin-rays of the ventral lobe of the caudal fin, while in neither type are they modified to support the anal fin, may be pointed out as a very strong argument in confirmation of their homology.

The demonstration of the homology of the hæmal arches of the tail in *Lepidosteus*

* "Beiträge z. vergl. Morph. d. Skeletsystems d. Wirbelthiere. II. Die Wirbelsäule u. ihre Anhänge." Archiv. f. Mikr. Anat., vol. xv., 1878, and vol. xvi., 1879.

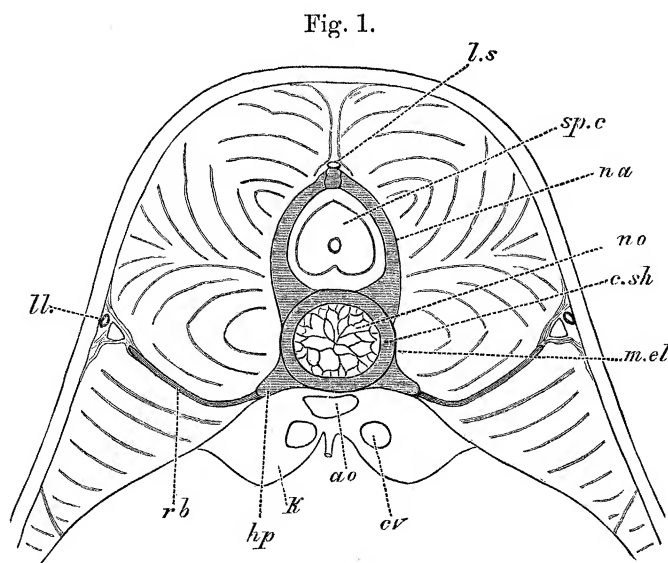
† "Ü. d. Entwick. d. Wirbelsäule d. *Lepidosteus*, mit. vergl. Anat. Bemerkungen." Jenaische Zeitschrift, Bd. iii., 1863.

‡ 'Comparative Embryology,' vol. ii., pp. 462, 463.

and Elasmobranchii might at first sight be taken as a conclusive argument in favour of GÖTTE's view, that the ribs of Elasmobranchii are not homologous with those of Ganoidei. This view is mainly supported by two facts :—

(1) In the first place, the ribs in Elasmobranchii do not at first sight appear to be serially homologous with the ventral parts of the hæmal arches of the tail, but would rather seem to be lateral offshoots of the hæmal processes, while the hæmal arches of the tail appear to be completed by the coalescence of independent ventral prolongations of the hæmal processes.

(2) In the second place, the position of the ribs is different in the two groups. In Elasmobranchii they are situated between the dorso-lateral and ventro-lateral muscles (woodcut, fig. 1, *rb.*), while in *Lepidosteus* and other Ganoids they immediately girth the body-cavity.



Diagrammatic section through the trunk of an advanced embryo of *Scyllium*, to show the position of the ribs.

ao., aorta; *c.sh.*, cartilaginous notochordal sheath; *cv.*, cardinal vein; *hp.*, hæmal process; *k.*, kidney; *l.s.*, ligamentum longitudinale superius; *m.el.*, membrana elastica externa; *na.*, neural arch; *no.*, notochord; *ll.*, lateral line; *rb.*, rib; *sp.c.*, spinal cord.

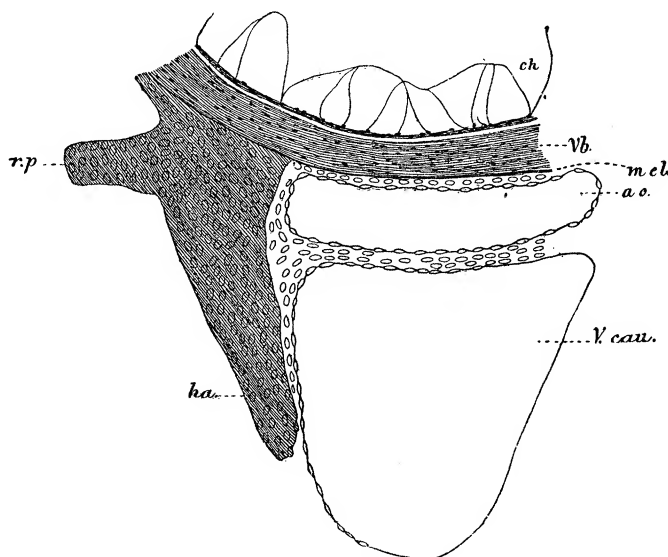
There is much, therefore, to be said in favour of GÖTTE's view. At the same time, there is another possible interpretation of the facts which would admit the homology of the ribs as well as of the hæmal arches throughout the Pisces.

Let us suppose, to start with, that the primitive arrangement of the parts is more or less nearly that found in *Lepidosteus*, where we have well-developed ribs in the region of the trunk, girding the body-cavity, and uniting in the caudal region to form the ventral parts of the hæmal arches. It is easy to conceive that the ribs in the trunk might somewhat alter their position by passing into the muscles, along the inter-muscular septa, till they come to lie between the dorso-lateral and ventro-lateral muscles, as in Elasmobranchii. *Lepidosteus* itself affords a proof that such a change

in the position of the ribs is not impossible, in that it differs from other Ganoids and from Teleostei in the fact that the free ends of the ribs leave the neighbourhood of the body-cavity and penetrate into the muscles.

If it be granted that the mere difference in position between the ribs of Ganoids and Elasmobranchii is not of itself sufficient to disprove their homology, let us attempt to picture what would take place at the junction of the trunk and tail in a type in which the ribs had undergone the above change in position. On nearing the tail it may be supposed that the ribs would gradually become shorter, and at the same time alter their position, till finally they shaded off into ordinary hæmal processes. If, however, the hæmal canal became prolonged forwards by the formation of some additional complete or nearly complete hæmal arches, an alteration in the relation of the parts would necessarily take place. Owing to the position of the ribs, these structures could hardly assist in the new formation of the anterior part of the hæmal canal, but the continuation forwards of the canal would be effected by prolongations of the hæmal processes supporting the ribs. The new arches so formed would naturally be held to be homologous with the hæmal arches of the tail, though really not so, while the true nature of the ribs would also be liable to be misinterpreted, in that the ribs would appear to be lateral outgrowths of the hæmal processes of a wholly different nature to the ventral parts of the hæmal arches of the tail.

Fig. 2.



Transverse section through the ventral part of the notochord, and adjoining structures of an advanced *Scyllium* embryo at the root of the tail.

Vb., cartilaginous sheath of the notochord; *ha.*, hæmal process; *r.p.*, process to which the rib is articulated; *m.el.*, membrana elastica externa; *ch.*, notochord; *ao.*, aorta; *V.cau.*, caudal vein.

In some Elasmobranchii, as shown in the accompanying woodcut (fig. 2), in the transitional vertebræ between the trunk and the tail, the ribs are supported by lateral

outgrowths of the hæmal processes, while the wholly independent prolongations of the hæmal processes appear to be about to give rise to the hæmal arches of the tail.

This peculiar state of things led GÖTTE, and subsequently one of us, to deny for Elasmobranchs all homology between the ribs and any part of the hæmal arches of the tail; but in view of the explanation just suggested, this denial was perhaps too hasty.

We are the more inclined to take this view because the researches of GÖTTE appear to show that an occurrence, in many respects analogous, has taken place in some Teleostei.

In Teleostei, JOHANNES MÜLLER, and following him GEGENBAUR, do not admit that the hæmal arches of the tail are in any part formed by the ribs. GEGENBAUR ('Elements of Comp. Anat.,' translation, p. 431) says, "In the Teleostei, the costiferous transverse processes" (what we have called the hæmal processes) "gradually converge in the caudal region, and form inferior arches, which are not homologous with those of Selachii and Ganoidei, although they also form spinous processes."

The opposite view, that the hæmal arches of the tail in Teleostei contain parts serially homologous with the basal parts of the hæmal processes as well as with the ribs, has been also maintained by many anatomists, *e.g.*, MECKEL, AUG. MÜLLER, &c., and has recently found a powerful ally in GÖTTE.

In many cases, the relations of the parts appear to be fundamentally those found in *Lepidosteus* and *Amia*, and GÖTTE has shown by his careful embryological investigations on *Esox* and *Anguilla*, that in these two forms there is practically conclusive evidence that the ribs as well as the hæmal costiferous processes of GEGENBAUR, which support them, enter into the formation of the hæmal arches of the tail.

In a great number of Teleostei, *e.g.*, the Salmon and most Cyprinoids, &c., the hæmal arches in the region of transition from the trunk to the tail have a structure which at first sight appears to support JOHANNES MÜLLER'S and GEGENBAUR'S view. The hæmal processes grow larger and meet each other ventrally; while the ribs articulated to them gradually grow smaller and disappear.

The Salmon is typical in this respect, and has been carefully studied by GÖTTE, who attempts to show (with, in our opinion, complete success) that the anterior hæmal arches are really not entirely homologous with the true hæmal arches behind, but that in the latter, the closure of the arch below is effected by the hæmal spine, which is serially homologous with a pair of coalesced ribs, while in the anterior hæmal arches, *i.e.*, those of the trunk, the closure of the arch is effected by a bridge of bone uniting the hæmal processes.

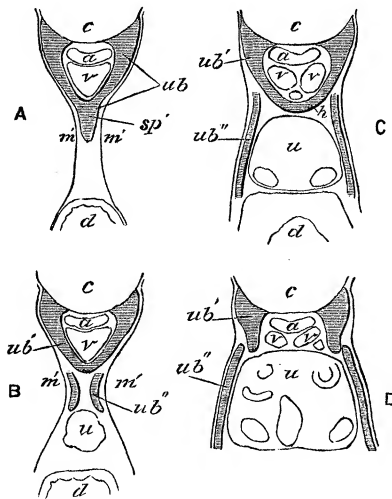
The arrangement of the parts just described, as well as the view of GÖTTE with reference to them, will be best understood from the accompanying woodcut (fig. 3), copied from GÖTTE'S memoir.

GÖTTE sums up his own results on this point in the following words (p. 138): "It follows from this, that the half rings, forming the hæmal canal in the hindermost trunk vertebræ of the Salmon, are not (with the exception of the last) completely

homologous with those of the tail, but are formed by a connecting piece between the basal stumps (hæmal processes), which originates as a paired median process of these stumps."

The incomplete homology between the anterior hæmal arches and the true caudal hæmal arches which follow them is exactly what we suggest may be the case in Elasmobranchii, and if it be admitted in the one case, we see no reason why it should not also be admitted in the other.

Fig. 3.



Semi-diagrammatic transverse sections through the first caudal vertebra (A), the last trunk vertebra (B), and the two trunk vertebrae in front (C and D), of a Salmon embryo of 2-3 centims. (From GÖTTE.)

ub., hæmal arch; *ub'*, hæmal process; *ub''*, rib; *c.*, notochord; *a.*, aorta; *v.*, vein; *h.*, connecting pieces between hæmal processes; *u.*, kidney; *d.*, intestine; *sp'*, hæmal spine; *m'*, muscles.

If this admission is made, the only ground for not regarding the ribs of Elasmobranchii as homologous with those of Ganoids is their different position, and we have already attempted to prove that this is not a fundamental point.

The results of our researches appear to us, then, to leave two alternatives as to the ribs of Fishes. One of these, which may be called GÖTTE'S view, may be thus stated:—The hæmal arches are homologous throughout the Pisces: in Teleostei, Ganoidei, and Dipnoi,* the ribs, placed on the inner face of the body-wall, are serially homologous with the ventral parts of the hæmal arches of the tail; in Elasmobranchii, on the other hand, the ribs are neither serially homologous with the hæmal arches of the tail nor homologous with the ribs of Teleostei and Ganoidei, but are outgrowths of the hæmal processes into the space between the dorso-lateral and ventro-lateral

* We find the serial homology of the ribs and ventral parts of the hæmal arches to be very clear in *Ceratodus*. WIEDERSHEIM states that it is not clear in *Protopterus*, although he holds that the facts are in favour of this view.

muscles, which may perhaps have their homologues in Teleostei and Ganoids in certain accessory processes of the vertebrae.

The other view, which we are inclined to adopt, and the arguments for which have been stated in the preceding pages, is as follows:—The Teleostei, Ganoidei, Dipnoi, and Elasmobranchii are provided with homologous hæmal arches, which are formed by the coalescence below the caudal vein of simple prolongations of the primitive hæmal processes of the embryo. The canal enclosed by the hæmal arches can be demonstrated embryologically to be the aborted body cavity.

In the region of the trunk the hæmal processes and their prolongations behave somewhat differently in the different types. In Ganoids and Dipnoi, in which the most primitive arrangement is probably retained, the ribs are attached to the hæmal processes, and are placed immediately without the peritoneal membrane at the insertions of the intermuscular septa. These ribs are in many instances (*Lepidosteus*, *Acipenser*), and very probably in all, developed continuously with the hæmal processes, and become subsequently segmented from them. They are serially homologous with the ventral parts of the hæmal arches of the tail, which, like them, are in many instances (*Ceratodus*, *Lepidosteus*, *Polypterus*, and to some extent in *Amia*) segmented off from the basal parts of the hæmal arches.

In Teleostei the ribs have the same position and relations as those in Ganoids and Dipnoi, but their serial homology with the ventral parts of the hæmal processes of the tail, is often (*e.g.*, the Salmon) obscured by some of the anterior hæmal arches in the posterior part of the trunk being completed, not by the ribs, but by independent outgrowths of the basal parts of the hæmal processes.

In Elasmobranchii a still further divergence from the primitive arrangement is present. The ribs appear to have passed outwards along the intermuscular septa into the muscles, and are placed between the dorso-lateral and ventro-lateral muscles (a change of position of the ribs of the same nature, but affecting only their ends, is observable in *Lepidosteus*). This change of position, combined probably with the secondary formation of a certain number of anterior hæmal arches similar to those in the Salmon, renders their serial homology with the ventral parts of the hæmal processes of the tail far less clear than in other types, and further proof is required before such homology can be considered as definitely established.

This is not the place to enter into the obscure question as to how far the ribs of the Amphibia and Amniota are homologous with those of Fishes. It is to be remarked, however, that the ribs of the Urodela (1) occupy the same position in relation to the muscles as the Elasmobranch ribs, (2) that they are connected with the neural arches, and (3) that they coexist in the tail with the hæmal arches, and seem, therefore, to be as different as possible from the ribs of the Dipnoi.

Part IV.—*The skeleton of the ventral lobe of the tail fin, and its bearing on the nature of the tail fin of the various types of Pisces.*

In the embryos or larvæ of all the Elasmobranchii, Ganoidei, and Teleostei which have up to this time been studied, the unpaired fins arise as median longitudinal folds of the integument on the dorsal and ventral sides of the body, which meet at the apex of the tail. The tail at first is symmetrical, having a form which has been called diphyccercal or protocercal. At a later stage, usually, though not always, parts of these fins atrophy, while other parts undergo a special development and constitute the permanent unpaired fins.

Since the majority of existing as well as extinct Fishes are provided with discontinuous fins, those forms, such as the Eel (*Anguilla*), in which the fins are continuous, have probably reverted to an embryonic condition: an evolutionary process which is of more frequent occurrence than has usually been admitted.

In the caudal region there is almost always developed in the larvæ of the above groups a special ventral lobe of the embryonic fin a short distance from the end of the tail. In Elasmobranchii and Chondrostean Ganoids the portion of the embryonic tail behind this lobe persists through life, and a special type of caudal fin, which is usually called heterocercal, is thus produced. This type of caudal fin appears to have been the most usual in the earlier geological periods.

Simultaneously with the formation of the ventral lobe of the heterocercal caudal fin, the notochord with the vertebral tissues surrounding it, becomes bent somewhat dorsally, and thus the primitive caudal fin forms a dorsally directed lobe of the heterocercal tail. We shall call this part the dorsal lobe of the tail-fin, and the secondarily formed lobe the ventral lobe.

Lepidosteus and *Amia* (WILDER, No. 15) amongst the bony Ganoids, and, as has recently been shown by A. AGASSIZ,* most Teleostei acquire at an early stage of their development heterocercal caudal fins, like those of Elasmobranchii and the Chondrostean Ganoids; but in the course of their further growth the dorsal lobe partly atrophies, and partly disappears as such, owing to the great prominence acquired by the ventral lobe. A portion of the dorsally flexed notochord and of the cartilage or bone replacing or investing it remains, however, as an indication of the original dorsal lobe, though it does not project backwards beyond the level of the end of the ventral lobe, which in these types forms the terminal caudal fin.

The true significance of the dorsally flexed portion of the vertebral axis was first clearly stated by HUXLEY,† but as A. AGASSIZ has fairly pointed out in the paper already quoted, this fact does not in any way militate against the view put forward by

* "On the Young Stages of some Osseous Fishes.—I. The Development of the Tail," Proc. of the American Academy of Arts and Sciences, vol. xiii., 1877.

† "Observations on the Development of some Parts of the Skeleton of Fishes," Quart. Journ. of Microsc. Science, vol. vii., 1859.

L. AGASSIZ that there is a complete parallelism between the embryonic development of the tail in these Fishes and the palæontological development of this organ. We think that it is moreover convenient to retain the term homocercal for those types of caudal fin in which the dorsal lobe has atrophied so far as not to project beyond the ventral lobe.

We have stated these now well-known facts to enable the reader to follow us in dealing with the comparison between the skeleton supporting the fin-rays of the ventral lobe of the caudal fin, and that supporting the fin-rays of the remaining unpaired fins.

It has been shown that in *Lepidosteus* the unpaired fins fall into two categories, according to the nature of the skeletal parts supporting them. The fin-rays of the true ventral lobe of the caudal fin are supported by the spinous processes of certain of the hæmal arches. The remaining unpaired fins, including the anal fin, are supported by the so-called interspinous bones, which are developed independently of the vertebral column and its arches.

The question which first presents itself is, how far does this distinction hold good for other Fishes? This question, though interesting, does not appear to have been greatly discussed by anatomists. Not unfrequently the skeletal supports of the ventral lobe of the caudal fin are assumed to be the same as those of the other fins.

DAVIDOFF,* for instance, in speaking of the unpaired fins of Elasmobranch embryos, says (p. 514): "The cartilaginous rays of the dorsal fins agreed not only in number with the spinous processes (as indeed is also found in the caudal fin of the full-grown Dog-fish)," &c.

THACHER,† again, in his memoir on the Median and Paired Fins, states at p. 284: "We shall here consider the skeleton of the dorsal and anal fins alone. That of the caudal fin has undergone peculiar modifications by the union of fin-rays with hæmal spines."

MIVART‡ goes into the question more fully. He points out (p. 471) that there is an essential difference between the dorsal and ventral parts of the caudal fin in Elasmobranchs, in that in the former the radials are more numerous than the vertebræ and unconformable to them, while in the latter they are equal in number to the vertebræ and continuous with them. "This," he goes on to say, "seems to point to a difference in nature between the dorsal and ventral portions of the caudal fin, in at least most Elasmobranchs." He further points out that *Polyodon* resembles Elasmobranchs. As to Teleostei, he does not express himself decidedly except in the case of *Muraena*, to which we shall return.

MIVART expresses himself as very doubtful as to the nature of the supports of the caudal fin, and thinks "that the caudal fin of different kinds of Fishes may have arisen in different ways in different cases."

* "Beiträge z. vergl. Anat. d. hinteren Gliedmassen d. Fische," *Morph. Jahrbuch*, vol. v., 1879.

† *Trans. of the Connecticut Acad.*, vol. iii., 1877.

‡ ST. GEORGE MIVART, "Fins of Elasmobranchs." *Zool. Trans.*, vol. x.

An examination of the ventral part of the caudal fin in various Ganoids, Teleostei, and Elasmobranchii appears to us to show that there can be but little doubt that, in the majority of the members of these groups at any rate, and we believe in all, the same distinction between the ventral lobe of the caudal fin and the remaining unpaired fins is found as in *Lepidosteus*.

In the case of most Elasmobranchii, a simple inspection of the caudal fin suffices to prove this, and the anatomical features involved in this fact have usually been recognised; though, in the absence of embryological evidence, the legitimate conclusion has not always been drawn from them.

The difference between the ventral lobe of the caudal fin and the other fins in the mode in which the fin-rays are supported is as obvious in Chondrostean Ganoids as it is in Elasmobranchii; it would appear also to hold good for *Amia*. *Polypterus* we have had no opportunity of examining, but if, as there is no reason to doubt, the figure of its skeleton given by AGASSIZ ('Poissons Fossiles') is correct, there can be no question that the ventral lobe of the caudal fin is supported by the hæmal arches, and not by interspinous bones. In *Calamoichthys*, the tail of which we have had an opportunity of dissecting through the kindness of Professor PARKER, the fin-rays of the ventral lobe of the true caudal fin are undoubtedly supported by true hæmal arches.

There is no unanimity of opinion as to the nature of the elements supporting the fin-rays of the caudal fin of Teleostei.

HUXLEY,* in his paper on the development of the caudal fin of the Stickleback, holds that these elements are of the nature of interhæmal bones. He says (p. 39): "The last of these rings lay just where the notochord began to bend up. It was slightly longer than the bony ring which preceded it, and instead of having its posterior margin parallel with the anterior, it sloped from above downwards and backwards. Two short osseous plates, attached to the anterior part of the inferior surface of the penultimate ring, or rudimentary vertebral centrum, passed downwards and a little backwards, and abutted against a slender elongated mass of cartilage. Similar cartilaginous bodies occupy the same relation to corresponding plates of bone in the anterior vertebræ in the region of the anal fin; and it is here seen, that while the bony plates coalesce and form the inferior arches of the caudal vertebræ, the cartilaginous elements at their extremities become the interhæmal bones. The cartilage connected with the inferior arch of the penultimate centrum is therefore an 'interhæmal' cartilage. The anterior part of the inferior surface of the terminal ossification likewise has its osseous inferior arch, but the direction of this is nearly vertical, and though it is connected below with an element which corresponds in position with the interhæmal cartilage, this cartilage is five or six times as large, and constitutes a broad vertical plate, longer than it is deep, and having its longest axis inclined downwards and backwards. . . .

* "Observations on the Development of some parts of the Skeleton of Fishes." Quart. Journ. Micr. Science, vol. vii., 1859.

"Immediately behind and above this anterior hypural apophysis (as it may be termed) is another very much smaller vertical cartilaginous plate, which may be called the posterior hypural apophysis."

We have seen that MIVART expresses himself doubtful on the subject. GEGENBAUR* appears to regard them as hæmal arches.

The latter view appears to us without doubt the correct one. An examination of the tail of normal Teleostei shows that the fin-rays of that part of the caudal fin which is derived from the ventral lobe of the larva are supported by elements serially homologous with the hæmal arches, but in no way homologous with the interspinous bones of the anal fin. The elements in question formed of cartilage in the larva, become ossified in the adult, and are known as the hypural bones. They may appear in the form of a series of separate hæmal arches, corresponding in number with the primitive somites of this region, which usually, however, atrophy in the adult, or more often are from the first imperfectly segmented, and have in the adult the form of two or three or even of a single broad bony plate. The transitional forms between this state of things and that, for instance, in *Lepidosteus* are so numerous, that there can be no doubt that even the most peculiar forms of the hypural bones of Teleostei are simply modified hæmal arches.

This view of the hypural bones is, moreover, supported by embryological evidence, since AUG. MÜLLER† (p. 205) describes their development in a manner which, if his statements are to be trusted, leaves no doubt on this point.

There are a considerable number of Fishes which are not provided with an obvious caudal fin as distinct from the remaining unpaired fins, *i.e.*, Chimæra, Eels, and various Eel-like forms amongst Teleostei, and the Dipnoi. GEGENBAUR appears to hold that these Fishes ought to be classed together in relation to the structure of the caudal portion of their vertebral column, as he says on p. 431 of his 'Comparative Anatomy' (English translation): "In the Chimæra, Dipnoi, and many Teleostei, the caudal portion of the vertebral column ends by gradually diminishing in size, but in most Fishes, &c."

For our purpose it will, however, be advisable to treat them separately.

The tail of Chimæra appears to us to be simply a peculiar modification of the typical Elasmobranch heterocercal tail, in which the true ventral lobe of the caudal fin may be recognised in the fin-fold immediately in front of the filamentous portion of the tail. In the allied genus *Callorhyncus* this feature is more distinct. The filamentous portion of the tail of Chimæra constitutes, according to the nomenclature adopted above, the true dorsal lobe, and may be partially paralleled in the filamentous dorsal lobe of the tail of the larval *Lepidosteus* (Plate 21, fig. 16).

The tail of the eel-like Teleostei is again undoubtedly a modification of the

* 'Elements of Comparative Anatomy.' (Translation), p. 431.

† "Beobachtungen zur vergl. Anat. d. Wirbelsäule." MÜLLER's Archiv., 1853.

normal form of tail characteristic of the Teleostei, in which, however, the caudal fin has become very much reduced and merged into the prolongations of the anal and dorsal fins.

This can be very clearly seen in Siluroid forms with an Eel-like tail, such as *Cnidoglanis*. Although the dorsal and ventral fins appear to be continuous round the end of the tail, and there is superficially no distinct caudal fin, yet an examination of the skeleton of *Cnidoglanis* shows that the end of the vertebral column is modified in the usual Teleostean fashion, and that the hæmal arches of the modified portion of the vertebral column support a small number of fin-rays; the adjoining ventral fin-rays being supported by independent osseous fin-supports (interspinous bones).

In the case of the Eel (*Anguilla anguilla*) HUXLEY (*loc. cit.*) long ago pointed out that the terminal portion of the vertebral column was modified in an analogous fashion to that of other Teleostei, and we have found that the modified hæmal arches of this part support a few fin-rays, through a still smaller number than in *Cnidoglanis*. The fin-rays so supported clearly constitute an aborted ventral lobe of the caudal fin.

Under these circumstances we think that the following statement by MIVART (*Zool. Trans.* vol. x., p. 471) is somewhat misleading:—

“As to the condition of this part (*i.e.*, the ventral lobe of the tail fin) in Teleosteans generally, I will not venture as yet to say anything generally, *except that it is plain that in such forms as Muræna, the dorsal and ventral parts of the caudal fin are similar in nature and homotypal with ordinary dorsal and anal fins.*”*

The italicized portion of this sentence is only true in respect to that part of the fringe of fin surrounding the end of the body, which is not only homotypal with, but actually part of, the dorsal and anal fins.

Having settled, then, that the tails of Chimæra and of Eel-like Teleostei are simply special modifications of the typical form of tail of the group of Fishes to which they respectively belong, we come to the consideration of the Dipnoi, in which the tail fin presents problems of more interest and greater difficulty than those we have so far had to deal with.

The undoubtedly very ancient and primitive character of the Dipnoi has led to the view, implicitly if not definitely stated in most text-books, that their tail-fin retains the character of the piscine tail prior to the formation of the ventral caudal lobe, a stage which is repeated embryologically in the pre-heterocercal condition of the tail in ordinary Fishes.

Through the want of embryological data, and in the absence of really careful histological examination of the tail of any of the Dipnoi, we are not willing to speak with very great confidence as to its nature; we are nevertheless of the opinion that the facts we can bring forward on this head are sufficient to show that the tail of the existing Dipnoi is largely aborted, so that it is more or less comparable with that of the Eel.

* The italics are ours.

We have had opportunities of examining the structure of the tail of *Ceratodus* and *Protopterus* in dissected specimens in the Cambridge Museum. The vertebral axis runs to the ends of the tail without showing any signs of becoming dorsally flexed. At some distance from the end of the tail the fin-rays are supported by what are apparently segmented spinous prolongations of the neural and hæmal arches. The dorsal elements are placed above the longitudinal dorsal cord, and occupy therefore the same position as the independent elements of the neural arches of *Lepidosteus*. They are therefore to be regarded as homologous with the dorsal fin-supports or interspinous bones of other types. The corresponding ventral elements are therefore also to be regarded as interspinous bones.

In view of the fact that the fin-supports, whenever their development has been observed, are found to be formed independently of the neural and hæmal arches, we may fairly assume that this is also true for what we have identified as the interspinous elements in the Dipnoi.

The interspinous elements become gradually shorter as the end of the tail is approached, and it is very difficult from a simple examination of dissected specimens to make out how far any of the posterior fin-rays are supported by the hæmal arches only. To this question we shall return, but we may remark that, although there is a prolongation backwards of the vertebral axis beyond the last interspinous elements, composed it would seem of the coalesced neural and hæmal arches but without the notochord, yet by far the majority of the fin-rays which constitute the apparent caudal fin are supported by interspinous elements.

The grounds on which we hold that the tail of the Dipnoi is to be regarded as a degenerate rather than primitive type of tail are the following:—

(1) If it be granted that a diphycercal or protocercal form of tail must have preceded a heterocercal form, it is also clear that the ventral fin-rays of such a tail must have been supported, as in *Polypterus* and *Calamoichthys*, by hæmal arches, and not by interspinous elements; otherwise, a special ventral lobe, giving a heterocercal character to the tail, and provided with fin-rays supported only by hæmal arches, could never have become evolved from the protocercal tail fin. Since the ventral fin-rays of the tail of the Dipnoi are supported by interspinous elements and not by hæmal arches, this tail fin cannot claim to have the character of *that* primitive type of diphycercal or protocercal tail from which the heterocercal tail must be supposed to have been evolved.

(2) Since the nearest allies of the Dipnoi are to be found in *Polypterus* and the Crassopterygidæ of HUXLEY, and since in these forms (as evinced by the structure of the tail fin of *Polypterus*, and the transitional type between a heterocercal and diphycercal form of fin observable in fossil Crassopterygidæ) the ventral fin-rays of the caudal fin were clearly supported by hæmal arches and not by interspinous elements, it is rendered highly probable that the absence of fin-rays so supported in the Dipnoi is a result of degeneration of the posterior part of the tail.

[We use this argument without offering any opinion as to whether the diphyccercal character of the tail of many Crassopterygidae is primary or secondary.]

(3) The argument just used is supported by the degenerate and variable state of the end of the vertebral axis in the Dipnoi—a condition most easily explained by assuming that the terminal part of the tail has become aborted.

(4) We believe that in *Ceratodus* we have been able to trace a small number of the ventral fin-rays supported by hæmal arches only, but these rays are so short as not to extend so far back as some of the rays attached to the interspinous elements in front. These rays may probably be interpreted, like the more or less corresponding rays in the tail of the Eel, as the last remnant of a true caudal fin.

The above considerations appear to us to show with very considerable probability that the true caudal fin of the Dipnoi has become all but aborted like that of various Teleostei; and that the apparent caudal fin is formed by the anal and dorsal fins meeting round the end of the stump of the tail.

From the adult forms of Dipnoi we are, however, of opinion that no conclusion can be drawn as to whether their ancestors were provided with a diphyccercal or a heterocercal form of caudal fin.

The general conclusions with reference to the tail fin at which we have arrived are the following:—

(1) The ventral lobe of the tail-fin of Pisces differs from the other unpaired fins in the fact that its fin-rays are directly supported by spinous processes of certain of the hæmal arches instead of independently developed interspinous bones.

(2) The presence or absence of fin-rays in the tail fin supported by hæmal arches may be used in deciding whether apparently diphyccercal tail fins are aborted or primitive.

EXCRETORY AND GENERATIVE ORGANS.

I.—*Anatomy.*

The excretory organs of *Lepidosteus* have been described by MÜLLER (No. 13) and HYRTL (No. 11). These anatomists have given a fairly adequate account of the generative ducts in the female, and HYRTL has also described the male generative ducts and the kidney and its duct, but his description is contradicted by our observations in some of the most fundamental points.

In the female example of 100·5 centims. which we dissected, the kidney forms a paired gland, consisting of a narrow strip of glandular matter placed on each side of the vertebral column, on the dorsal aspect of the body cavity. It is covered on its ventral aspect by the oviduct and by its own duct, but is separated from both of these by a layer of the tough peritoneal membrane, through which the collecting tubes pass. It extends forwards from the anus for about three-fifths of the length of the body-cavity, and in our example had a total length of about 28 centims. (Plate 26, fig. 60, *k*).

Anteriorly the two kidneys are separated by a short interval in the median line, but posteriorly they come into contact, and are so intimately united as almost to constitute a single gland.

A superficial examination might lead to the supposition that the kidney extended forwards for the whole length of the body-cavity up to the region of the branchial arches, and HYRTL appears to have fallen into this error; but what appears to be its anterior continuation is really a form of lymphatic tissue, something like that of the spleen, filled with numerous cells. This matter (Plate 26, fig. 60, *ly.*) continues from the kidney forwards without any break, and has a colour so similar to that of the kidney as to be hardly distinguishable from it with the naked eye. The true anterior end of the kidney is placed about 3 centims. in front on the left side, and on the same level on the right side as the wide anterior end of the generative duct (Plate 26, fig. 60, *od.*). It is not obviously divided into segments, and is richly supplied with malpighian bodies.

It is clear from the above description that there is no trace of head-kidney or pronephros visible in the adult. To this subject we shall, however, again return.

As will appear from the embryological section, the ducts of the kidneys are probably simply the archinephric ducts, but to avoid the use of terms involving a theory, we propose in the anatomical part of our work to call them kidney ducts. They are thin-walled widish tubes coextensive with the kidneys. If cut open there may be seen on their inner aspect the numerous openings of the collecting tubes of the kidneys. They are placed ventrally to and on the outer border of the kidneys (Plate 26, fig. 60, *sg.*). Posteriorly they gradually enlarge, and approaching each other in the median line, coalesce, forming an unpaired vesicle or bladder (*bl.*)—about 6 centims. long in our example—opening by a median pore on a more or less prominent papilla (*u.g.*) behind the anus. The dilated portions of the two ducts are called by HYRTL the horns of the bladder.

The sides of the bladder and its so-called horns are provided with lateral pockets into which the collecting tubes of the kidney open. These pockets, which we have found in two female examples, are much larger in the horns of the bladder than in the bladder itself. Similar pockets, but larger than those we have found, have been described by HYRTL in the male, but are stated by him to be absent in the female. It is clear from our examples that this is by no means always the case.

HYRTL states that the wide kidney ducts, of which his description differs in no material point from our own, suddenly narrow in front, and, perforating the peritoneal lining, are continued forwards to supply the anterior part of the kidney. We have already shown that the anterior part of the kidney has no existence, and the kidney ducts supplying it are, according to our investigations, equally imaginary.

It was first shown by MÜLLER, whose observations on this point have been confirmed by HYRTL, &c., that the ovaries of *Lepidosteus* are continuous with their ducts, forming in this respect an exception to other Ganoids.

In our example of *Lepidosteus* the ovaries (Plate 26, fig. 60, *ov.*) were about 18

centims. in length. They have the form of simple sacs, filled with ova, and attached about their middle to their generative duct, and continued both backwards and forwards from their attachment into a blind process.

With reference to these sacs MÜLLER has pointed out—and the importance of this observation will become apparent when we deal with the development—that the ova are formed in the thickness of the inner wall of the sac. We hope to show that the inner wall of the sac is alone equivalent to the genital ridge of, for instance, the ovary of *Scyllium*. The outer aspect of this wall—i.e., that turned towards the interior of the sac—is equivalent to the outer aspect of the Elasmobranch genital ridge, on which alone the ova are developed.* The sac into which the ova fall is, as we shall show in the embryological section, a special section of the body-cavity shut off from the remainder, and the dehiscence of the ova into this cavity is equivalent to their discharge into the body cavity in other forms.

The oviduct (Plate 26, fig. 60, *od.*) is a thin-walled duct of about 21 centims. in length in the example we are describing, continuous in front with the ovarian sac, and gradually tapering behind, till it ends (*od'.*) by opening into the dilated terminal section of the kidney duct on the inner side, a short distance before the latter unites with its fellow. It is throughout closely attached to the ureter and placed on its inner, and to some extent on its ventral, aspect. The hindermost part of the oviduct which runs beside the enlarged portion of the kidney duct—that portion called by HYRTL the horn of the urinary bladder—is so completely enveloped by the wall of the horn of the urinary bladder as to appear like a projection into the lumen of the latter structure, and the somewhat peculiar appearance which it presents in HYRTL'S figure is due to this fact. In our examples the oviduct was provided with a simple opening into the kidney duct, on a slight papilla; the peculiar dilatations and processes of the terminal parts of the oviduct, which have been described by HYRTL, not being present.

The results we have arrived at with reference to the male organs are very different indeed from those of our predecessor, in that we find *the testicular products to be carried off by a series of vasa efferentia, which traverse the mesorchium, and are continuous with the uriniferous tubuli; so that the semen passes through the uriniferous tubuli into the kidney duct and so to the exterior. We have moreover been unable to find in the male a duct homologous with the oviduct of the female.*

This mode of transportation outwards of the semen has not hitherto been known to occur in Ganoids, though found in all Elasmobranchii, Amphibia, and Amniota. It is not, however, impossible that it exists in other Ganoids, but has hitherto been overlooked.

Our male example of *Lepidosteus* was about 60 centims. in length, and was no doubt mature. It was smaller than any of our female examples, but this according to GARMAN (vide, p. 361) is usual. The testes (Plate 26, fig. 58 A, *t.*) occupied a similar position to the ovaries, and were about 21 centims. long. They were, as is frequently

* 'Treatise on Comparative Embryology,' vol. i., p. 43.

the case with piscine testes, divided into a series of lobes (10–12), and were suspended by a delicate mesentery (mesorchium) from the dorsal wall of the abdomen on each side of the dorsal aorta. HYRTL (No. 11) states that air or quicksilver injected between the limbs of the mesentery, passed into a vas deferens homologous with the oviduct which joins the ureter. We have been unable to find such a vas deferens; but we have found in the mesorchium a number of tubes of a yellow colour, the colour being due to a granular substance quite unlike coagulated blood, but which appeared to us from microscopic examination to be the remains of spermatozoa.* These tubes to the number of 40–50 constitute, we believe, the vasa efferentia. Along the line of suspension of the testis on its inner border these tubes unite to form an elaborate network of tubes placed on the inner face of the testis—an arrangement very similar to that often found in Elasmobranchii (vide F. M. BALFOUR, ‘Monograph on the Development of Elasmobranch Fishes,’ plate 19, figs. 4 and 8).

We have figured this network on the posterior lobe of the testis (fig. 58 B), and have represented a section through it (fig. 59 A, *n.v.e.*), and through one of the vasa efferentia (*v.e.*) in the mesorchium. Such a section conclusively demonstrates the real nature of these passages: they are filled with sperm like that in the body of the testis, and are, as may be seen from the section figured, continuous with the seminal tubes of the testis itself.

At the attached base of the mesorchium the vasa efferentia unite into a longitudinal canal, placed on the inner side of the kidney duct (Plate 26, fig. 58 A, *l.c.*, also shown in section in Plate 26, fig. 59 B, *l.c.*). From this canal tubules pass off which are continuous with the tubuli uriniferi, as may be seen from fig. 59 B, but the exact course of these tubuli through the kidney could not be made out in the preparations we were able to make of the badly conserved kidney. HYRTL describes the arrangement of the vascular trunks in the mesorchium in the following way (No. 11, p. 6): “The mesorchium contains vascular trunks, viz., veins, which through their numerous anastomoses form a plexus at the hilus of the testis, whose efferent trunks, 13 in number, again unite into a plexus on the vertebral column, which is continuous with the cardinal veins.” The arrangement (though not the number) of HYRTL’s vessels is very similar to that of our vasa efferentia, and we cannot help thinking that a confusion of the two may have taken place; which, in badly conserved specimens, not injected with semen, would be very easy.

We have, as already stated, been unable to find in our dissections any trace of a duct homologous with the oviduct of the female, and our sections through the kidney and its ducts equally fail to bring to light such a duct. The kidney ducts are about 19 centims. in length, measured from the genital aperture to their front end. These ducts are generally similar to those in the female; they unite about 2 centims. from

* The females we examined, which were no doubt procured at the same time as the male, had their oviducts filled with ova: and it is therefore not surprising that the vasa efferentia should be naturally injected with sperm.

the genital pore to form an unpaired vesicle. Their posterior parts are considerably enlarged, forming what HYRTL calls the horns of the urinary bladder. In these enlarged portions, and in the wall of the unpaired urinary bladder, numerous transverse partitions are present, as correctly described by HYRTL, which are similar to those in the female, but more numerous. They give rise to a series of pits, at the blind ends of which are placed the openings of the kidney tubules. The kidney duct without doubt serves as vas deferens, and we have found in it masses of yellowish colour similar to the substance in the vasa efferentia identified by us as remains of spermatozoa.

II.—*Development.*

In the general account of the development we have already called attention to the earliest stages of the excretory system.

We may remind the reader that the first part of the system to be formed is the segmental or archinephric duct (Plate 23, figs. 28 and 29, *sg.*). This duct arises, as in Teleostei and Amphibia, by the constriction of a hollow ridge of the somatic mesoblast into a canal, which is placed in contiguity with the epiblast, along the line of junction between the mesoblastic somites and the lateral plates of mesoblast. Anteriorly the duct does not become shut off from the body-cavity, and also bends inwards towards the middle line. The inflected part of the duct is the first rudiment of the pronephros, and very soon becomes considerably dilated relatively to the posterior part of the duct.

The posterior part of each segmental duct acquires an opening into the cloacal section of the alimentary tract. Apart from this change, the whole of the ducts, except their pronephric sections, remain for a long time unaltered, and the next changes we have to speak of concern the definite establishment of the pronephros.

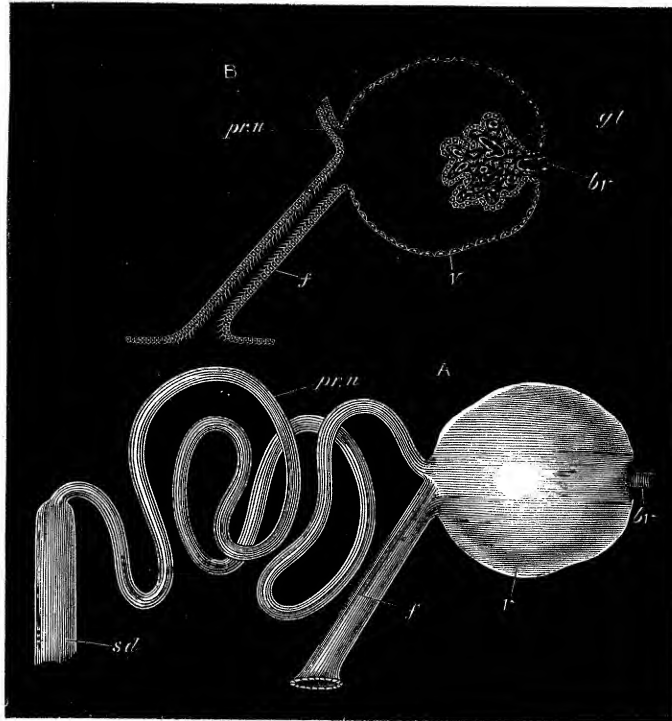
The dilated incurved portion of each segmental duct soon becomes convoluted, and by the time the embryo is about 10 millims. in length, but before the period of hatching, an important change is effected in the relations of their peritoneal openings.*

Instead of leading into the body-cavity, they open into an isolated chamber on each side (Plate 25, fig. 51, *pr.c.*), which we will call the *pronephric chamber*. The pronephric chamber is not, however, so far as we can judge, completely isolated from the body-cavity. We have not, it is true, detected with certainty at this stage a communication between the two; but in later stages, in larvæ of from 11 to 26 millims., we have found a richly ciliated passage leading from the body-cavity into the pronephros on each side (Plate 25, fig. 52, *p.f.p.*). We have not succeeded in determining with absolute certainty the exact relations between this passage and the tube of the pronephros, but we are inclined to believe that it opens directly into the pronephric chamber just spoken of.

* The change is probably effected somewhat earlier than would appear from our description, but our specimens were not sufficiently well preserved to enable us to speak definitely as to the exact period.

As we hope to show, this chamber soon becomes largely filled by a vascular glomerulus. On the accomplishment of these changes, the pronephros is essentially provided with all the parts typically present in a segment of the mesonephros (woodcut, fig. 4). There is a peritoneal tube (*f.*),* opening into a vesicle (*v.*); from near the neck of the peritoneal tube there comes off a convoluted tube (*pr.n.*), forming the main mass of the pronephros, and ending in the segmental duct (*sd.*).

Fig. 4.

Diagrammatic views of the pronephros of *Lepidosteus*.

A, pronephros supposed to be isolated and seen from the side; B, section through the vesicle of the pronephros and the ciliated peritoneal funnel leading into it; *pr.n.*, coiled tube of pronephros; *sd.*, segmental or archinephric duct; *f.*, peritoneal funnel; *v.*, vesicle of pronephros; *bv.*, blood vessel of glomerulus; *gl.*, glomerulus.

The different parts do not, however, appear to have the same morphological significance as those in the mesonephros.

Judging from the analogy of Teleostei, the embryonic structure of whose pronephros is strikingly similar to that of *Lepidosteus*, the two pronephric chambers into which the segmental ducts open are constricted off sections of the body-cavity.

With the formation of the convoluted duct opening into the isolated section of

* We feel fairly confident that there is only one pronephric opening on each side, though we have no single series of sections sufficiently complete to demonstrate this fact with absolute certainty.

the body-cavity we may speak of a definite pronephros as having become established. The pronephros is placed, as can be made out in later stages, on the level of the opening of the air-bladder into the throat.

The pronephros increases in size, so far as could be determined, by the further convolution of the duct of which it is mainly formed; and the next change of importance which we have noticed is the formation of a vascular projection into the pronephric chamber, forming the glomerulus already spoken of (*vide* woodcut, fig. 4, *gl.*), which is similar to that of the pronephros of Teleostei. We first detected these glomeruli in an embryo of about 15 millims., some days after hatching (Plate 25, fig. 52, *gl.*), but it is quite possible that they may be formed considerably earlier.

In the same embryo in which the glomeruli were found we also detected for the first time a *mesonephros* consisting of a series of isolated segmental or nephridial tubes, placed posteriorly to the pronephros along the dorsal wall of the abdomen.

These were so far advanced at this stage that we are not in a position to give any account of their mode of origin. They are, however, formed independently of the segmental ducts, and in the establishment of the junction between the two structures, there is no outgrowth from the segmental duct to meet the segmental tubes. We could not at this stage find peritoneal funnels of the segmental tubes, though we have met with them at a later stage (Plate 25, fig. 53, *p.f.*), and our failure to find them at this stage is not to be regarded as conclusive against their existence.

A very considerable space exists between the pronephros and the foremost segmental tube of the mesonephros. The anterior mesonephric tubes are, moreover, formed earlier than the posterior.

In the course of further development, the mesonephric tubules increase in size, so that there ceases to be an interval between them, the mesonephros thus becoming a continuous gland. In an embryo of 26 millims. there was no indication of the formation of segmental tubes to fill up the space between the pronephros and mesonephros.

The two segmental ducts have united behind into an unpaired structure in an embryo of 11 millims. This structure is no doubt the future unpaired urinogenital chamber (Plate 26, figs. 58 A, and 60, *bl.*). Somewhat later, the hypoblastic cloaca becomes split into two sections, the hinder one receiving the coalesced segmental ducts, and the anterior remaining continuous with the alimentary tract. The opening of the hinder one forms the urinogenital opening, and that of the anterior the anus.

In an older larva of about 5.5 centims. the pronephros did not exhibit any marked signs of atrophy, though the duct between it and the mesonephros was somewhat reduced and surrounded by the trabecular tissue spoken of in connexion with the adult. In the region between the pronephros and the front end of the fully developed part of the mesonephros very rudimentary tubules had become established.

The latest stage of the excretory system which we have studied is in a young Fish of about 11 centims. in length. The special interest of this stage depends upon the

fact that the ovary is already developed, and not only so, but the formation of the oviducts has commenced, and their condition at this stage throws considerable light on the obscure problem of their nature in the Ganoids.

Unfortunately, the head of the young Fish had been removed before it was put into our hands, so that it was impossible for us to determine whether the pronephros was still present; but as we shall subsequently show, the section of the segmental duct, originally present between the pronephros and the front end of the permanent kidney or mesonephros, has in any case disappeared.

In addition to an examination of the excretory organs *in situ*, which showed little except the presence of the generative ridges, we made a complete series of sections through the excretory organs for their whole length (Plate 26, figs. 54-57).

Posteriorly these sections showed nothing worthy of note, the excretory organs and their ducts differing in no important particular from these organs as we have described them in the adult, except in the fact that the segmental ducts are not joined by the oviducts.

Some little way in front of the point where the two segmental ducts coalesce to form the urinary bladder, the genital ridge comes into view. For its whole extent, except near its anterior part (of which more hereafter) this ridge projects freely into the body-cavity, and in this respect the young Fish differs entirely from the adult. As shown in Plate 26, figs. 56 and 57 (*g.r.*), it is attached to the abdominal wall on the ventral side of, and near the inner border of each kidney. The genital ridge itself has a structure very similar to that which is characteristic of young Elasmobranchii, and it may be presumed of young Fishes generally. The free edge of the ridge is swollen, and this part constitutes the true generative region of the ridge, while its dorsal portion forms the supporting mesentery. The ridge itself is formed of a central stroma and a germinal epithelium covering it. The epithelium is thin on the whole of the inner aspect of the ridge, but, just as in Elasmobranchii, it becomes greatly thickened for a band-like strip on the outer aspect. Here, the epithelium is several layers deep, and contains numerous primitive germinal cells (*p.o.*).

Though the generative organs were not sufficiently advanced for us to decide the point with certainty, the structure of the organ is in favour of the view that this specimen was a female, and, as will be shown directly, there can on other grounds be no doubt that this is so. The large size of the primitive germinal cells (primitive ova) reminded us of these bodies in Elasmobranchii.

In the region between the insertion of the genital ridge (or ovary, as we may more conveniently call it) and the segmental duct we detected the openings of a series of peritoneal funnels of the excretory tubes (Plate 26, fig. 57, *p.f.*), which clearly therefore persist till the young Fish has reached a very considerable size.

As we have already said, the ovary projects freely into the body-cavity for the greater part of its length. Anteriorly, however, we found that a lamina extended from the free ventral edge of the ovary to the dorsal wall of the body-cavity, to which

it was attached on the level of the outer side of the segmental duct. A somewhat triangular channel was thus constituted, the inner wall of which was formed by the ovary, the outer by the lamina just spoken of, and the roof by the strip of the peritoneum of the abdominal wall covering that part of the ventral surface of the kidney in which the openings of the peritoneal funnels of the excretory tubes are placed. The structure of this canal will be at once understood by the section of it shown in Plate 26, fig. 55.

There can be no doubt that this canal is the commencing ovarian sac. On tracing it backwards we found that the lamina forming its outer wall arises as a fold growing upwards from the free edge of the genital ridge meeting a downward growth of the peritoneal membrane from the dorsal wall of the abdomen; and in Plate 26, fig. 56, these two laminae may be seen before they have met. Anteriorly the canal becomes gradually smaller and smaller in correlation with the reduced size of the ovarian ridge, and ends blindly nearly on a level with the front end of the excretory organs.

It should be noted that, owing to the mode of formation of the ovarian sac, the outer side of the ovary with the band of thickened germinal epithelium is turned towards the lumen of the sac; and thus the fact of the ova being formed on the inner wall of the genital sac in the adult is explained, and the comparison which we instituted in our description of the adult between the inner wall of the genital sac and the free genital ridge of Elasmobranchs receives its justification.

It is further to be noticed that, from the mode of formation of the ovarian sac, the openings of the peritoneal funnels of the excretory organs ought to open into its lumen; and if these openings persist in the adult, they will no doubt be found in this situation.

Before entering on further theoretical considerations with reference to the oviduct, it will be convenient to complete our description of the excretory organs at this stage.

When we dissected the excretory organs out, and removed them from the body of the young Fish, we were under the impression that they extended for the whole length of the body-cavity. Great was our astonishment to find that slightly in front of the end of the ovary both excretory organs and segmental ducts grew rapidly smaller and finally vanished, and that what we had taken to be the front part of the kidney was nothing else but a linear streak of tissue formed of cells with peculiar granular contents supported in a trabecular work (Plate 26, fig. 54). This discovery first led us to investigate histologically what we, in common with previous observers, had supposed to be the anterior end of the kidneys in the adult, and to show that they were nothing else but trabecular tissue with cells like that of lymphatic glands. The interruption of the segmental duct at the commencement of this tissue demonstrates that if any rudiment of the pronephros still persists, it is quite functionless, in that it is not provided with a duct.

III.—*Theoretical considerations.*

There are three points in our observations on the urinogenital system which appear to call for special remark. The first of these concerns the structure and fate of the pronephros, the second the nature of the oviduct, and the third the presence of vasa efferentia in the male.

Although the history we have been able to give of the pronephros is not complete, we have nevertheless shown that in most points it is essentially similar to the pronephros of Teleostei. In an early stage we find the pronephros provided with a peritoneal funnel opening into the body-cavity. At a later stage we find that there is connected with the pronephros on each side, a cavity—the pronephric cavity—into which a glomerulus projects. This cavity is in communication on the one hand with the lumen of the coiled tube which forms the main mass of the pronephros, and on the other hand with the body-cavity by means of a richly ciliated canal (woodcut, fig. 4, p. 416).

In Teleostei the pronephros has precisely the same characters, except that the cavity in which the glomerulus is placed is without a peritoneal canal.

The questions which naturally arise in connexion with the pronephros are: (1) what is the origin of the above cavity with its glomerulus; and (2) what is the meaning of the ciliated canal connecting this cavity with the peritoneal cavity?

We have not from our researches been able to answer the first of these questions. In Teleostei, however, the origin of this cavity has been studied by ROSENBERG* and GÖTTE†. According to the account of the latter, which we have not ourselves confirmed but which has usually been accepted, the front end of the segmental duct, instead of becoming folded off from the body-cavity, becomes included in a kind of diverticulum of the body-cavity, which only communicates with the remainder of the body-cavity by a narrow opening. On the inner wall of this diverticulum a projection is formed which becomes a glomerulus. At this stage in the development of the pronephros we have essentially the same parts as in the fully formed pronephros of *Lepidosteus*, the only difference being that the passage connecting the diverticulum containing the glomerulus with the remainder of the body-cavity is short in Teleostei, and in *Lepidosteus* forms a longish ciliated canal. In Teleostei the opening into the body-cavity becomes soon closed. If the above comparison is justified, and if the development of these parts in *Lepidosteus* takes place as it is described as doing in Teleostei, there can, we think, be no doubt that the ciliated canal of *Lepidosteus*, which connects the pronephric cavity with the body-cavity, is a persisting communication between this cavity and the body-cavity; and that *Lepidosteus* presents in this respect a more primitive type of pronephros than Teleostei.

It may be noted that in *Lepidosteus* the whole pronephros has exactly the character of a single segmental tube of the mesonephros. The pronephric cavity with its

* ROSENBERG, Untersuch. üb. d. Entwickl. d. Teleostierneiere. Dorpat, 1867.

† GÖTTE, Entwickl. d. Unke, p. 826.

glomerulus is identical in structure with a malpighian body. The ciliated canal is similar in its relations to the peritoneal canal of such a segmental tube, and the coiled portion of the pronephros resembles the secreting part of the ordinary segmental tube. This comparison is no doubt an indication that the pronephros is physiologically very similar to the mesonephros, and so far justifies SEDGWICK'S* comparison between the two, but it does not appear to us to justify the morphological conclusions at which he has arrived, or to necessitate any modification in the views on this subject expressed by one of us.†

The genital ducts of Ganoids and Teleostei have for some time been a source of great difficulty to morphologists; and any contributions with reference to the ontogeny of these structures are of interest.

The essential point which we have made out is that the anterior part of the oviduct of *Lepidosteus* arises by a fold of the peritoneum attaching itself to the free edge of the genital ridge. We have not, unfortunately, had specimens old enough to decide how the posterior part of the oviduct is formed; and although in the absence of such stages it would be rash in the extreme to speak with confidence as to the nature of this part of the duct, it may be well to consider the possibilities of the case in relation to other Ganoids and Teleostei.

The simplest supposition would be that the posterior part of the genital duct had the same origin as the anterior, *i.e.*, that it was formed for its whole length by the concrescence of a peritoneal fold with the genital ridge, and that the duct so formed opened into the segmental duct.

The other possible supposition is that a true Müllerian duct—*i.e.*, a product of the splitting of the segmental duct—is subsequently developed, and that the open end of this duct coalesces with the duct which has already begun to be formed in our oldest larva.

In attempting to estimate the relative probability of these two views, one important element is the relation of the oviducts of *Lepidosteus* to those of other Ganoids.

In all other Ganoids (vide HYRTL, No. 11) there are stated to be genital ducts in both sexes which are provided at their anterior extremities with a funnel-shaped mouth open to the abdominal cavity. At first sight, therefore, it might be supposed that they had no morphological relationship with the oviducts of *Lepidosteus*, but, apart from the presence of a funnel-shaped mouth, the oviducts of *Lepidosteus* are very similar to those of Chondrostean Ganoids, being thin-walled tubes opening on a projecting papilla into the dilated kidney ducts (horns of the urinary bladder, HYRTL). These relations seem to prove beyond a doubt that the oviduct of *Lepidosteus* is for its major part homologous with the genital ducts of other Ganoids.

* SEDGWICK, "Early Development of the Wolffian Duct and anterior Wolffian Tubules in the Chick; with some Remarks on the Vertebrate Excretory System." Quart. Jour. of Micros. Science, vol. xxi., 1881.

† F. M. BALFOUR, 'Comparative Embryology,' vol. ii., pp. 600-603.

The relationship of the genital ducts to the kidney ducts in *Amia* and *Polypterus* is somewhat different from that in the Chondrostei and *Lepidosteus*. In *Amia* the ureters are so small that they may be described rather as joining the coalesced genital ducts than *vice versa*, although the apparent coalesced portion of the genital ducts is shown to be really part of the kidney ducts by receiving the secretion of a number of mesonephric tubuli. In *Polypterus* the two ureters are stated to unite, and open by a common orifice into a sinus formed by the junction of the two genital ducts, which has not been described as receiving directly the secretion of any part of the mesonephros.

It has been usual to assume that the genital ducts of Ganoids are true Müllerian ducts in the sense above defined, on the ground that they are provided with a peritoneal opening and that they are united behind with the kidney ducts. In the absence of ontological evidence this identification is necessarily provisional. On the assumption that it is correct we should have to accept the second of the two alternatives above suggested as to the development of the posterior parts of the oviduct in *Lepidosteus*.

There appear to us, however, to be sufficiently serious objections to this view to render it necessary for us to suspend our judgment with reference to this point. In the first place, if the view that the genital ducts are Müllerian ducts is correct, the true genital ducts of *Lepidosteus* must necessarily be developed at a later period than the secondary attachment between their open mouths and the genital folds, which would, to say the least of it, be a remarkable inversion of the natural order of development. Secondly, the condition of our oldest larva shows that the Müllerian duct, if developed later, is only split off from quite the posterior part of the segmental duct; yet in all types in which the development of the Müllerian duct has been followed, its anterior extremity, with the abdominal opening, is split off from either the foremost or nearly the foremost part of the segmental duct.

Judging from the structure of the adult genital duct of other Ganoids they must also be developed only from the posterior part of the segmental duct, and this peculiarity so struck one of us that in a previous paper* the suggestion was put forward that the true Ganoid genital ducts were perhaps not Müllerian ducts, but enlarged segmental tubes with persisting abdominal funnels belonging to the mesonephros.

If the possibility of the oviduct of *Lepidosteus* not being a Müllerian duct is admitted, a similar doubt must also exist as to the genital ducts of other Ganoids, and we must be prepared to show that there is a reasonable ground for scepticism on this point. We would in this connexion point out that the second of the two arguments urged against the view that the genital duct of *Lepidosteus* is not a Müllerian duct applies with equal force to the case of all other Ganoids.

The short funnel-shaped genital duct of the Chondrostei is also very unlike

* F. M. BALFOUR, "On the Origin and History of the Urinogenital Organs of Vertebrates," Journ. of Anat. and Phys., vol. x., 1876.

undoubted Müllerian ducts, and could moreover easily be conceived as originating by a fold of the peritoneum, a slight extension of which would give rise to a genital duct like that of *Lepidosteus*.

The main difficulty of the view that the genital ducts of Ganoids are not Müllerian ducts lies in the fact that they open into the segmental duct. While it is easy to understand the genesis of a duct from a folding of the peritoneum, and also easy to understand how such a duct might lead to the exterior by coalescing, for instance, with an abdominal pore, it is not easy to see how such a duct could acquire a communication with the segmental duct.

We do not under these circumstances wish to speak dogmatically, either in favour of or against the view that the genital ducts of Ganoids are Müllerian ducts. Their ontogeny would be conclusive on this matter, and we trust that some of the anatomists who have the opportunity of studying the development of the Sturgeon will soon let us know the facts of the case. If there are persisting funnels of the mesonephric segmental tubes in adult Sturgeons, some of them ought to be situated within the genital ducts, if the latter are not Müllerian ducts; and naturalists who have the opportunity ought also to look out for such openings.

The mode of origin of the anterior part of the genital duct of *Lepidosteus* appears to us to tell strongly in favour of the view, already regarded as probable by one of us,* that the Teleostean genital ducts are derived from those of Ganoids; and if, as appears to us indubitable, the most primitive type of Ganoid genital ducts is found in the Chondrostei, it is interesting to notice that the remaining Ganoids present in various ways approximations to the arrangement typically found in Teleostei. *Lepidosteus* obviously approaches Teleostei in the fact of the ovarian ridge forming part of the wall of the oviduct, but differs from the Teleostei in the fact of the oviduct opening into the kidney ducts, instead of each pair of ducts having an independent opening in the cloaca, and in the fact that the male genital products are not carried to the exterior by a duct homologous with the oviduct. *Amia* is closer to the Teleostei in the arrangement of the posterior part of the genital ducts, in that the two genital ducts coalesce posteriorly; while *Polypterus* approaches still nearer to the Teleostei in the fact that the two genital ducts and the two kidney ducts unite with each other before they join; and in order to convert this arrangement into that characteristic of the Teleostei we have only to conceive the coalesced ducts of the kidneys acquiring an independent opening into the cloaca behind the genital opening.

The male genital ducts.—The discovery of the vasa efferentia in *Lepidosteus*, carrying off the semen from the testis, and transporting it to the mesonephros, and thence through the mesonephric tubes to the segmental duct, must be regarded as the most important of our results on the excretory system.

It proves in the first place that the transportation outwards of the genital products of both sexes by homologous ducts, which has been hitherto held to be universal in

* F. M. BALFOUR, 'Comparative Embryology,' vol. ii., p. 605.

Ganoids, and which, in the absence of evidence to the contrary, must still be assumed to be true for all Ganoids except *Lepidosteus*, is a secondary arrangement. This conclusion follows from the fact that in Elasmobranchs, &c., which are not descendants of the Ganoids, the same arrangement of seminal ducts is found as in *Lepidosteus*, and it must therefore have been inherited from an ancestor common to the two groups.

If, therefore, the current statements about the generative ducts of Ganoids are true, the males must have lost their vasa efferentia, and the function of vas deferens must have been taken by the homologue of the oviduct, presumably present in the male. The Teleostei must, moreover, have sprung from Ganoidei in which the vasa efferentia had become aborted.

Considerable phylogenetic difficulties as to the relationships of Ganoidei and Elasmobranchii are removed by the discovery that Ganoids were originally provided with a system of vasa efferentia like that of Elasmobranchii.

THE ALIMENTARY CANAL AND ITS APPENDAGES.

I.—*Anatomy.*

AGASSIZ (No. 2) gives a short description with a figure of the viscera of *Lepidosteus* as a whole. VAN DER HÖVEN has also given a figure of them in his memoir on the air-bladder of this form (No. 8), and JOHANNES MÜLLER first detected the spiral valve and gave a short account of it in his memoir (No. 13). STANNIUS, again, makes several references to the viscera of *Lepidosteus* in his anatomy of the Vertebrata, and throws some doubt on MÜLLER's determination of the spiral valve.

The following description refers to a female *Lepidosteus* of 100·5 centims. (Plate 27, fig. 66).

With reference to the mouth and pharynx, we have nothing special to remark. Immediately behind the pharynx there comes an elongated tube, which is not divisible into stomach and œsophagus, and may be called the stomach (*st.*). It is about 44·6 centims. long, and gradually narrows from the middle towards the hinder or pyloric extremity. It runs straight backwards for the greater part of its length, the last 3·8 centims., however, taking a sudden bend forwards. For about half its length the walls are thin, and the mucous membrane is smooth; in the posterior half the walls are thick, and the mucous membrane is raised into numerous longitudinal ridges. The peculiar glandular structure of the epithelium of this part in the embryo is shown in Plate 27, fig. 62 (*st.*). Its opening into the duodenum is provided with a very distinct pyloric valve (*py.*). This valve projects into a kind of chamber, freely communicating with the duodenum, and containing four large pits (*c'*), into each of which a group of pyloric cæca opens. These cæca form a fairly compact gland (*c.*) about 6·5 centims. long, which overlaps the stomach anteriorly, and the duodenum posteriorly.

Close to the pyloric valve, on its right side, is a small papilla, on the apex of which the bile duct opens (*b.d'*).

A small, apparently glandular, mass closely connected with the bile duct, in the position in which we have seen the pancreas in the larva (Plate 27, figs. 62 and 63, *p.*), is almost certainly a rudimentary pancreas, like that of many Teleostei; but its preservation was too bad for histological examination. We believe that the pancreas of *Lepidosteus* has hitherto been overlooked.

The small intestine passes straight backwards for about 8 centims., and then presents three compact coils. From the end of these a section, about 5 centims. long, the walls of which are much thicker, runs forwards. The intestine then again turns backwards, making one spiral coil. This spiral part passes directly, without any sharp line of demarcation, into a short and straight tube, which tapers slightly from before backwards, and ends at the anus. The mucous membrane of the intestine for about the first 3.5 centims. is smooth, and the muscular walls thin: the rest of the small intestine has thick walls, and the mucous membrane is reticulated.

A short spiral valve (*sp.v.*), with a very rudimentary epithelial fold, making nearly two turns, begins in about the posterior half of the spiral coil of the intestine, extending backwards for slightly less than half the straight terminal portion of the intestine, and ending 4 centims. in front of the anus. Its total length in one example was about 4.5 centims.

The termination of the spiral valve is marked by a slight constriction, and we may call the straight portion of the intestine behind it the rectum (*rc.*).

The posterior part of the intestine, from the beginning of the spiral valve to the anus, is *connected with the ventral wall of the abdomen by a mesentery.*

The air-bladder (*a.b.*) is 45 centims. long, and opens into the alimentary canal by a slit-like aperture (*a.b'*) on the median dorsal line, immediately behind the epipharyngeal teeth. Each lip of this aperture is largely formed by a muscular cushion, thickest at its posterior end, and extending about 6 millims. behind the aperture itself. A narrow passage is bounded by these muscular walls, which opens dorsally into the air-bladder.

The air-bladder is provided with two short anterior cornua, and tapers to a point behind: it shows no indication of any separation into two parts. A strong band of connective tissue runs along the inner aspect of its whole dorsal region, from which there are given off on each side—at intervals of about 12 millims. anteriorly, gradually increasing to 18 millims. posteriorly—bands of muscle, which pass outwards towards its side walls, and then spread out into the numerous reticulations with which the air-bladder is lined throughout. By the contraction of these muscles the cavity of the air-bladder can doubtless be very much diminished.

The main muscular bands circumscribe a series of more or less complete chambers, which were about twenty-seven in number on each side in our example. The chambers are confined to the sides, so that there is a continuous cavity running

through the central part of the organ. The whole organ has the characteristic structure of a simple lung.

The liver (*lr.*) consists of a single elongated lobe, about 32 centims. long, tapering anteriorly and posteriorly, the anterior half being on the average twice as thick as the posterior half. The gall-bladder (*g.b.*) lies at its posterior end, and is of considerable size, tapering gradually so as to pass insensibly into the bile duct. The hepatic duct (*hp.d.*) opens into the gall-bladder at its anterior end.

The spleen (*s.*) is a large, compact, double gland, one lobe lying in the turn of the intestine immediately above the spiral valve, and the other on the opposite side of the intestine, so that the intestine is nearly embraced between the two lobes.

II.—*Development.*

We have already described in detail the first formation of the alimentary tract so far as we have been able to work it out, and we need only say here that the anterior and posterior ends of the canal become first formed, and that these two parts gradually elongate, so as to approach each other; the growth of the posterior part is, however, the most rapid. The junction of the two parts takes place a very short distance behind the opening of the bile duct into the intestine.

For some time after the two parts of the alimentary tract have nearly met, the ventral wall of the canal at this point is not closed; so that there is left a passage between the alimentary canal and the yolk-sac, which forms a vitelline duct.

After the yolk-sac has ceased to be visible as an external appendage it still persists within the abdominal cavity. It has, however, by this stage ceased to communicate with the gut, so that the eventual absorption of the yolk is no doubt entirely effected by the vitelline vessels. At these later stages of development we have noticed that numerous yolk nuclei, like those met with in Teleostei and Elasmobranchii,* are still to be found in the yolk.

It will be convenient to treat the history of sections of the alimentary tract in front of and behind the vitelline duct separately. The former gives rise to the pharyngeal region, the œsophagus, the stomach, and the duodenum.

The pharyngeal region, immediately after it has become established, gives rise to a series of paired pouches. These may be called the branchial pouches, and are placed between the successive branchial arches. The first or hyomandibular pouch, placed between the mandibular and hyoid arches, has rather the character of a double layer of hypoblast than of a true pouch, though in parts a slight space is developed between its two walls. It is shown in section in Plate 24, fig. 43 (*h.m.*), from an embryo of about 10 millims., shortly before hatching. It does not appear to undergo any further development, and, so far as we can make out, disappears shortly after the embryo is hatched, without acquiring an opening to the exterior.

* For a history of similar nuclei, vide 'Comp. Embryol.,' vol. ii., chapters iii. and iv.

It is important to notice that this cleft, which in the cartilaginous Ganoids and *Polypterus* remains permanently open as the spiracle, is rudimentary even in the embryo of *Lepidosteus*.

The second pouch is the hyobranchial pouch: its outer end meets the epiblast before the larva is hatched, and a perforation is effected at the junction of the two layers, converting the pouch into a visceral cleft.

Behind the hyobranchial pouch there are four branchial pouches, which become perforated and converted into branchial clefts shortly after hatching.

The region of the œsophagus following the pharynx is not separated from the stomach, unless a glandular posterior region (vide description of adult) be regarded as the stomach, a non-glandular anterior region forming the œsophagus. The lumen of this part appears to be all but obliterated in the stages immediately before hatching, giving rise for a short period to a solid œsophagus like that of Elasmobranchii and Teleostei.*

From the anterior part of the region immediately behind the pharynx the air-bladder arises as a dorsal unpaired diverticulum. From the very first it has an elongated slit-like mouth (Plate 27, fig. 64, *a.b'*.), and is placed in the mesenteric attachment of the part of the throat from which it springs.

We have first noticed it in the stages immediately after hatching. At first very short and narrow, it grows in succeeding stages longer and wider, making its way backwards in the mesentery of the alimentary tract (Plate 27, fig. 65, *a.b.*). In the larva of a month and a half old (26 millims.) it has still a perfectly simple form, and is without traces of its adult lung-like structure; but in the larva of 11 centims. it has the typical adult structure.

The stomach is at first quite straight, but shortly after the larva is hatched its posterior end becomes bent ventralwards and forwards, so that the flexure of its posterior end (present in the adult) is very early established. The stomach is continuous behind with the duodenum, the commencement of which is indicated by the opening of the bile duct.

The liver is the first-formed alimentary gland, and is already a compact body before the larva is hatched. We have nothing to say with reference to its development, except that it exhibits the same simple structure in the embryo that it does in the adult.

A more interesting glandular body is the pancreas. It has already been stated that in the adult we have recognised a small body which we believe to be the pancreas, but that we were unable to study its histological characters.

In the embryo there is a well-developed pancreas which arises in the same position and the same manner as in those Vertebrata in which the pancreas is an important gland in the adult.

We have first noticed the pancreas in a stage shortly after hatching (Plate 27,

* Vide 'Comp. Embryol.,' vol. ii., pp. 50-63.

fig. 61, *p.*). It then has the form of a funnel-shaped diverticulum of the *dorsal* wall of the duodenum, immediately behind the level of the opening of the bile duct. From the apex of this funnel numerous small glandular tubuli soon sprout out.

The similarity in the development of the pancreas in *Lepidosteus* to that of the same gland in Elasmobranchii is very striking.*

The pancreas at a later stage is placed immediately behind the end of the liver in a loop formed by the pyloric section of the stomach (Plate 27, fig. 62, *p.*). During larval life it constitutes a considerable gland, the anterior end of which partly envelopes the bile duct (Plate 27, fig. 63, *p.*).

Considering the undoubted affinities between *Lepidosteus* and the Teleostei, the facts just recorded with reference to the pancreas appear to us to demonstrate that the small size and occasional absence (?) of this gland in Teleostei is a result of the degeneration of this gland; and it seems probable that the pancreas will be found in the larvæ of most Teleostei. These conclusions render intelligible, moreover, the great development of the pancreas in the Elasmobranchii.

We have first noticed the pyloric cæca arising as outgrowths of the duodenum in larvæ of about three weeks old, and they become rapidly longer and more prominent (Plate 27, fig. 62, *c.*).

The portion of the intestine behind the vitelline duct is, as in all the Vertebrata, at first straight. In Elasmobranchs the lumen of the part of the intestine in which a spiral valve is present in the adult, very early acquires a more or less semilunar form by the appearance of a fold which winds in a long spiral. In *Lepidosteus* there is a fold similar in every respect (Plate 25, fig. 53, *sp.v.*), forming an open spiral round the intestine. This fold is the first indication of the spiral valve, but it is relatively very much later in its appearance than in Elasmobranchs, not being formed till about three weeks after hatching. It is, moreover, in correlation with the small extent of the spiral valve of the adult, confined to a much smaller portion of the intestine than in Elasmobranchii, although owing to the relative straightness of the anterior part of the intestine it is proportionately longer in the embryo than in the adult.

The similarity of the embryonic spiral valve of *Lepidosteus* to that of Elasmobranchii shows that STANNIUS' hesititation in accepting MÜLLER's discovery of the spiral valve in *Lepidosteus* is not justified.

J. MÜLLER ('Bau u. Entwickl. d. Myxinoiden') holds that the so-called bursa entiana of Elasmobranchii (*i.e.*, the chamber placed between the part of the intestine with the spiral valve and the end of the pylorus) is the homologue of the more elongated portion of the small intestine which occupies a similar position in the Sturgeon. This portion of the small intestine is no doubt homologous with the still more elongated and coiled portion of the small intestine in *Lepidosteus* placed between the chamber into which the pyloric cæca, &c., open and the region of the spiral valve. The fact that the vitelline duct in the embryo *Lepidosteus* is placed close to the pyloric end of

* Vide F. M. BALFOUR, 'Monograph on Development of Elasmobranch Fishes,' p. 226.

the stomach, and that the greater portion of the small intestine is derived from part of the alimentary canal behind this, shows that MÜLLER is mistaken in attempting to homologise the bursa entiana of Elasmobranchii, which is placed in front of the vitelline duct, with the coiled part of the small intestine of the above forms. The latter is either derived from an elongation of the very short portion of the intestine between the vitelline duct and the primitive spiral valve, or more probably by the conversion of the anterior part of the intestine, originally provided with a spiral valve into a coiled small intestine not so provided.

We have already called attention to the peculiar mesentery present in the adult attaching the posterior straight part of the intestine to the ventral wall of the body. This mesentery, which together with the dorsal mesentery divides the hinder section of the body-cavity into two lateral compartments is, we believe, a persisting portion of the ventral mesentery which, as pointed out by one of us,* is primitively present for the whole length of the body-cavity. The persistence of such a large section of it as that found in the adult *Lepidosteus* is, so far as we know, quite exceptional. This mesentery is shown in section in the embryo in Plate 25, fig. 53 (*v.mt.*). The small vessel in it appears to be the remnant of the subintestinal vein.

THE GILL ON THE HYOID ARCH.

It is well known that *Lepidosteus* is provided with a gill on the hyoid arch, divided on each side into two parts. An excellent figure of this gill is given by MÜLLER (No. 13, plate 5, fig. 6), who holds from a consideration of the vascular supply that the two parts of this gill represent respectively the hyoid gill and the mandibular gill (called by MÜLLER pseudobranch). MÜLLER's views on this subject have not usually been accepted, but it is the fashion to regard the whole of the gill as the hyoid gill divided into two parts. It appeared to us not improbable that embryology might throw some light on the history of this gill, and accordingly we kept a look out in our embryos for traces of gills on the hyoid and mandibular arches. The results we have arrived at are purely negative, but are not the less surprising for this fact. The hyomandibular cleft as shown above, is never fully developed, and early undergoes a complete atrophy—a fact which is, on the whole, against MÜLLER's view; but what astonished us most in connexion with the gill in question is that we have been unable to find any trace of it even in the oldest larva whose head we have had (26 millims.), and at a period when the gills on the hinder arches have reached their full development.

We imagined the gill in question to be the remnant of a gill fully formed in extinct Ganoid types, and therefore expected to find it better developed in the larva than in the adult. That the contrary is the fact appears to us fairly certain, although we cannot at present offer any explanation of it.

* 'Comparative Embryology,' vol. ii., p. 514.

SYSTEMATIC POSITION OF LEPIDOSTEUS.

A. AGASSIZ concludes his memoir on the development of *Lepidosteus* by pointing out that in spite of certain affinities in other directions this form is "not so far removed from the bony Fishes as has been supposed." Our own observations go far to confirm AGASSIZ' opinion.

Apart from the complete segmentation, the general development of *Lepidosteus* is strikingly Teleostean. In addition to the general Teleostean features of the embryo and larva, which can only be appreciated by those who have had an opportunity of practically working at the subject, we may point to the following developmental features* as indicative of Teleostean affinities:—

- (1.) The formation of the nervous system as a solid keel of the epiblast.
- (2.) The division of the epiblast into a nervous and epidermic stratum.
- (3.) The mode of development of the gut (vide pp. 369, 370).
- (4.) The mode of development of the pronephros; though, as shown on p. 420, the pronephros of *Lepidosteus* has primitive characters not retained by Teleostei.
- (5.) The early stages in the development of the vertebral column (vide p. 388).

In addition to these, so to speak, purely embryonic characters there are not a few important adult characters:—

- (1.) The continuity of the oviducts with the genital glands.
- (2.) The small size of the pancreas, and the presence of numerous so-called pancreatic cæca.
- (3.) The somewhat coiled small intestine.
- (4.) Certain characters of the brain, *e.g.*, the large size of the cerebellum; the presence of the so-called lobi inferiores on the infundibulum; and of tori semi-circulares in the mid-brain.

In spite of the undoubtedly important list of features to which we have just called attention, a list containing not less important characters, both embryological and adult, separating *Lepidosteus* from the Teleostei, can be drawn up:—

- (1.) The character of the truncus arteriosus.
- (2.) The fact of the genital ducts joining the ureters.
- (3.) The presence of vasa efferentia in the male carrying the semen from the testes to the kidney, and through the tubules of the latter into the kidney duct.
- (4.) The presence of a well-developed opercular gill.
- (5.) The presence of a spiral valve; though this character may possibly break down with the extension of our knowledge.
- (6.) The typical Ganoid characters of the thalamencephalon and the cerebral hemispheres (vide pp. 381 and 382).
- (7.) The chiasma of the optic nerves.

* The features enumerated above are not in all cases confined to *Lepidosteus* and Teleostei, but are always eminently characteristic of the latter.

(8.) The absence of a pecten, and presence of a vascular membrane between the vitreous humour and the retina.

(9.) The opisthocœlous form of the vertebræ.

(10.) The articulation of the ventral parts of the hæmal arches of the tail with processes of the vertebral column.

(11.) The absence of a division of the muscles into dorso-lateral and ventro-lateral divisions.

(12.) The complete segmentation of the ovum.

The list just given appears to us sufficient to demonstrate that *Lepidosteus* cannot be classed with the Teleostei; and we hold that MÜLLER'S view is correct, according to which *Lepidosteus* is a true Ganoid.

The existence of the Ganoids as a distinct group has, however, recently been challenged by so distinguished an Ichthyologist as GÜNTHER, and it may therefore be well to consider how far the group as defined by MÜLLER is a natural one for living forms,* and how far recent researches enable us to improve upon MÜLLER'S definitions. In his classical memoir (No. 13) the characters of the Ganoids are thus shortly stated:—

“These Fishes are either provided with plate-like angular or rounded cement-covered scales, or they bear osseous plates, or are quite naked. The fins are often, but not always, beset with a double or single row of spinous plates or splints. The caudal fin occasionally embraces in its upper lobe the end of the vertebral column, which may be prolonged to the end of the upper lobe. Their double nasal openings resemble those of Teleostei. The gills are free, and lie in a branchial cavity under an operculum, like those of Teleostei. Many of them have an accessory organ of respiration, in the form of an opercular gill, which is distinct from the pseudobranch, and can be present together with the latter; many also have spiracles like Elasmobranchii. They have many valves in the stem of the aorta like the latter, also a muscular coat in the stem of the aorta. Their ova are transported from the abdominal cavity by oviducts. Their optic nerves do not cross each other. The intestine is often provided with a spiral valve, like Elasmobranchii. They have a swimming-bladder with a duct, like many Teleostei. Their pelvic fins are abdominal.

“If we include in a definition only those characters which are invariable, the Ganoids may be shortly defined as being those Fish with numerous valves to the stem of the aorta, which is also provided with a muscular coat; with free gills and an operculum, and with abdominal pelvic fins.”

To these distinctive characters, he adds in an appendix to his paper, the presence of the spiral valve, and the absence of a processus falciformis and a choroid gland.

* We do not profess to be able to discuss this question for extinct forms of Fish, though of course it is a necessary consequence of the theory of descent that the various groups should merge into each other as we go back in geological time.

To the distinctive set of characters given by MÜLLER we may probably add the following :—

(1.) Oviducts and urinary ducts always unite, and open by a common urinogenital aperture behind the anus.

(2.) Skull hyostylic.

(3.) Segmentation complete in the types so far investigated, though perhaps *Amia* may be found to resemble the Teleostei in this particular.

(5.) A pronephros of the Teleostean type present in the larva.

(6.) Thalamencephalon very large and well developed.

(7.) The ventricle in the posterior part of the cerebrum is not divided behind into lateral halves, the roof of the undivided part being extremely thin.

(8.) Abdominal pores always present.

The great number of characters just given are amply sufficient to differentiate the Ganoids as a group; but, curiously enough, the only characters amongst the whole series which have been given, which can be regarded as peculiar to the Ganoids, are (1) the characters of the brain, and (2) the fact of the oviducts and kidney ducts uniting together and opening by a common pore to the exterior.

This absence of characters peculiar to the Ganoids is an indication of how widely separated in organisation are the different members of this great group.

At the same time, the only group with which existing Ganoids have close affinities is the Teleostei. The points they have in common with the Elasmobranchii are merely such as are due to the fact that both retain numerous primitive Vertebrate characters,* and the gulf which really separates them is very wide.

There is again no indication of any close affinity between the Dipnoi and, at any rate, existing Ganoids.

Like the Ganoids, the Dipnoi are no doubt remnants of a very primitive stock; but in the conversion of the air-bladder into a true lung, the highly specialised character of their limbs,† their peculiar autostylic skulls, the fact of their ventral nasal openings leading directly into the mouth, their multisegmented bars (interspinous bars), directly prolonged from the neural and hæmal arches and supporting the fin-rays of the unpaired dorsal and ventral fins, and their well-developed cerebral hemispheres, very unlike those of Ganoids and approaching the Amphibian type, they form a very well-defined group, and one very distinctly separated from the Ganoids.

No doubt the Chondrosteian Ganoids are nearly as far removed from the Teleostei as from the Dipnoi, but the links uniting these Ganoids with the Teleostei have been so fully preserved in the existing fauna of the globe, that the two groups almost run

* As instances of this we may cite (1) the spiral valve; (2) the frequent presence of a spiracle; (3) the frequent presence of a communication between the pericardium and the body-cavity; (4) the heterocercal tail.

† Vide F. M. BALFOUR, "On the Development of the Skeleton of the Paired Fins of Elasmobranchs," Proc. Zool. Soc., 1881.

into each other. If, in fact, we were anxious to make any radical change in the ordinary classification of Fishes, it would be by uniting the Teleostei and Ganoids, or rather constituting the Teleostei into one of the sub-groups of the Ganoids, equivalent to the Chondrostei. We do not recommend such an arrangement, which in view of the great preponderance of the Teleostei amongst living Fishes would be highly inconvenient, but the step from *Amia* to the Teleostei is certainly not so great as that from the Chondrostei to *Amia*, and is undoubtedly less than that from the Selachii to the Holocephali.

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<i>a.</i>	Anus.	<i>d.l.</i>	Dorsal lobe of caudal fin.
<i>a.b.</i>	Air-bladder.	<i>dl.f.</i>	Dorsal fin.
<i>a.b'.</i>	Aperture of air-bladder into throat.	<i>e.</i>	Eye.
<i>a.c.</i>	Anterior commissure.	<i>ed.</i>	Epidermis.
<i>a.f.</i>	Anal fin.	<i>ep.</i>	Epiblast.
<i>al.</i>	Alimentary canal.	<i>f.b.</i>	Fore-brain.
<i>ao.</i>	Aorta.	<i>f.e.</i>	Pyriform bodies surrounding the zona radiata of the ovum, probably the remains of epithelial cells.
<i>ar.</i>	Artery.	<i>g.b.</i>	Gall-bladder.
<i>au.</i>	Auditory pit.	<i>g.d.</i>	Genital duct.
<i>b.</i>	Brain.	<i>gl.</i>	Glomerulus.
<i>b.c.</i>	Body-cavity.	<i>g.r.</i>	Genital ridge.
<i>b.d.</i>	Bile duct.	<i>h.</i>	Heart.
<i>b.d'.</i>	Aperture of bile duct into duodenum.	<i>h.a.</i>	Hæmal arch.
<i>bl.</i>	Coalesced portion of segmental ducts, forming urinogenital bladder.	<i>h.b.</i>	Hind-brain.
<i>br.a.</i>	Branchial arches.	<i>h.c.</i>	Head-cavity.
<i>br.c.</i>	Branchial clefts.	<i>hp.d.</i>	Hepatic duct.
<i>c.</i>	Pyloric cæca.	<i>h.m.</i>	Hyomandibular cleft.
<i>c'.</i>	Apertures of cæca into duodenum.	<i>h.op.</i>	Operculum.
<i>cb.</i>	Cerebellum.	<i>hy.</i>	Hypoblast ; in fig. 10, hyoid arch.
<i>cd.v.</i>	Cardinal vein.	<i>hyl.</i>	Hyaloid membrane.
<i>ce.</i>	Cerebrum : in figs. 47 A and B, anterior lobe of cerebrum.	<i>i.c.</i>	Intercalated cartilaginous elements of the neural arches.
<i>ce'.</i>	Posterior lobe of cerebrum.	<i>in.</i>	Infundibulum.
<i>c.f.</i>	Caudal fin.	<i>ir.</i>	Iris.
<i>cn.</i>	Centrum.	<i>i.s.</i>	Interspinous cartilage or bones.
<i>ch.</i>	Choroidal fissure.	<i>i.v.</i>	Sub-intestinal vein.
<i>cr.v.</i>	Circular vein of vascular membrane of eye.	<i>iv.r.</i>	Intervertebral ring of cartilage.
<i>c.sh.</i>	Cuticular sheath of notochord.	<i>k.</i>	Kidney.
<i>c.v.</i>	Caudal vein.	<i>l.</i>	Lens.
<i>d.</i>	Duodenum.	<i>l.c.</i>	Longitudinal canal, formed by union of the vasa efferentia.
<i>d.c.</i>	Dorsal cartilage of neural arch.	<i>l.in.</i>	Lobi inferiores.
<i>d.f.</i>	Dermal fin-rays.	<i>l.l.</i>	Ligamentum longitudinale superius.

<i>lr.</i>	Liver.	<i>pr.n.</i>	Pronephros.
<i>lt.</i>	Lateral line.	<i>pr.n'.</i>	Opening of pronephros into pronephric chamber.
<i>ly.</i>	Lymphatic body in front of kidney.	<i>pt.</i>	Pituitary body.
<i>m.</i>	Mouth.	<i>py.</i>	Pyloric valve.
<i>m.b.</i>	Mid-brain.	<i>p.z.</i>	Parietal zone of blastoderm.
<i>m.c.</i>	Medullary cord.	<i>r.</i>	Rostrum.
<i>m.el.</i>	Membrana elastica externa.	<i>rb.</i>	Rib.
<i>mes.</i>	Mesorchium.	<i>rc.</i>	Rectum.
<i>mn.</i>	Mandible.	<i>s.</i>	Spleen.
<i>md. and mo.</i>	Medulla oblongata.	<i>s.c.</i>	Seminal vessels passing from the longitudinal canal into the kidney.
<i>ms.</i>	Mesoblast.	<i>s.d.</i>	Suctorial disc.
<i>n.a.</i>	Neural arch.	<i>sg.</i>	Segmental or archinephric duct.
<i>n.a'.</i>	Dorsal element of neural arch.	<i>sg.t.</i>	Segmental tubules.
<i>nc.</i>	Notochord.	<i>sh.</i>	Granular outer portion of the sheath of the notochord in the vertebral regions.
<i>n.v.e.</i>	Network formed by vasa efferentia on inner face of testis.	<i>s.mx.</i>	Superior maxillary process.
<i>od.</i>	Oviduct.	<i>s.nc.</i>	Sub-notochordal rod.
<i>od'.</i>	Aperture of oviduct into bladder.	<i>so.</i>	Somatic mesoblast.
<i>ol.</i>	Nasal pit or aperture.	<i>sp.</i>	Splanchnic mesoblast.
<i>olf.</i>	Olfactory lobe.	<i>sp.n.</i>	Spinal nerve.
<i>op.</i>	Optic vesicle.	<i>sp.v.</i>	Spiral valve.
<i>op.ch.</i>	Optic chiasma.	<i>st.</i>	Stomach.
<i>op.l.</i>	Optic lobes.	<i>s.t.</i>	Seminal tubes of the testis.
<i>op.th.</i>	Optic thalami.	<i>su.p.</i>	Suctorial papillæ.
<i>or.ep.</i>	Oral epithelium.	<i>t.</i>	Testis.
<i>ov.</i>	Ovary.	<i>th.</i>	Thalamencephalon.
<i>p.</i>	Pancreas.	<i>th.l.</i>	Lobes of the roof of the thalamencephalon.
<i>pc.</i>	Pericardium.	<i>tr.</i>	Trabeculæ.
<i>pc.f.</i>	Pectoral fin.	<i>u.g.</i>	Urinogenital aperture.
<i>p.ch.</i>	Pigmented layer of choroid.	<i>v.</i>	Ventricle.
<i>p.f.</i>	Peritoneal funnel of segmental tube of mesonephros.	<i>v.e.</i>	Vasa efferentia.
<i>p.f.p.</i>	Peritoneal funnel leading into pronephric chamber.	<i>v.h.</i>	Vitreous humour.
<i>p.g.</i>	Pectoral girdle.	<i>v.l.</i>	Ventral lobe of the caudal fin.
<i>pl.f.</i>	Pelvic fin.	<i>v.mt.</i>	Ventral mesentery.
<i>pn.</i>	Pineal gland.	<i>vn.</i>	Vein.
<i>p.o.</i>	Primitive germinal cells.	<i>vs.</i>	Blood-vessel.
<i>pr.</i>	Mesoblastic somite.		
<i>pr.c.</i>	Pronephric chamber.		

<i>v.sh.</i>	Vascular sheath between the hyaloid membrane and the vitreous humour.	<i>z.r.</i>	Outer striated portion of investing membrane (zona radiata) of ovum.
<i>v.th.</i>	Vesicle of the thalamencephalon.	<i>z.r'.</i>	Inner non-striated portion of investing membrane of ovum.
<i>x.</i>	Groove in epiblast, probably formed in process of hardening.	I.	Olfactory nerve.
<i>y.</i>	Yolk.	II.	Optic nerve.
<i>z.</i>	Commissure in front of pineal gland.	III.	Oculomotor nerve.
		V.	Trigeminal nerve.
		VIII.	Facial and auditory nerves.

EXPLANATION OF FIGURES.

PLATE 21.

Figs. 1-4. Different stages in the segmentation of the ovum.

Fig. 1. Ovum with a single vertical furrow, from above.

Fig. 2. Ovum with two vertical furrows, from above.

Fig. 3. Side view of an ovum with a completely formed blastodermic disc.

Fig. 4. The same ovum as fig. 3, from below, showing four vertical furrows nearly meeting at the vegetative pole.

Figs. 5-10. External views of embryos up to time of hatching.

Fig. 5. Embryo, 3.5 millims. long, third day after impregnation.

Fig. 6. Embryo on the fifth day after impregnation.

Fig. 7. Posterior part of same embryo as fig. 6, showing tail swelling.

Fig. 8. Embryo on the sixth day after impregnation.

Fig. 9. Embryo on the seventh day after impregnation.

Fig. 10. Embryo on the eleventh day after impregnation (shortly before hatching).

Fig. 11. Head of embryo about the same age as fig. 10, ventral aspect.

Fig. 12. Side view of a larva about 11 millims. in length, shortly after hatching.

Fig. 13. Head of a larva about the same age as fig. 12, ventral aspect.

Fig. 14. Side view of a larva about 15 millims. long, five days after hatching.

Fig. 15. Head of a larva 23 millims. in length.

Fig. 16. Tail of a larva 11 centims. in length.

Fig. 17. Transverse section through the egg-membranes of a just-laid ovum.

We are indebted to Professor W. K. PARKER for figs. 12, 14, and 15.

PLATE 22.

Figs. 18-22. Transverse sections of embryo on the third day after impregnation.

Fig. 18. Through head, showing the medullary keel.

Fig. 19. Through anterior part of trunk.

Fig. 20. Through same region as fig. 19, showing a groove (*x.*) in the epiblast, probably artificially formed in the process of hardening.

Fig. 21. Through anterior part of tail region, showing partial fusion of layers.

Fig. 22. Through posterior part of tail region, showing more complete fusion of layers than fig. 21.

Figs. 23-25. Transverse sections of an embryo on the fifth day after impregnation.

Fig. 23. Through fore-brain and optic vesicles.

Fig. 24. Through hind-brain and auditory pits.

Fig. 25. Through anterior part of trunk.

Figs. 26-27. Transverse sections of the head of an embryo on the sixth day after impregnation.

Fig. 26. Through fore-brain and optic vesicles.

Fig. 27. Through hind-brain and auditory pits.

PLATE 23.

Figs. 28-29. Transverse sections of the trunk of an embryo on the sixth day after impregnation.

Fig. 28. Through anterior part of trunk (from a slightly older embryo than the other sections of this stage).

Fig. 29. Slightly posterior to fig. 28, showing formation of segmental duct as a fold of the somatic mesoblast.

Fig. 30. Longitudinal horizontal section of embryo on the sixth day after impregnation, passing through the mesoblastic somites, notochord, and medullary canal.

Figs. 31-34. Transverse sections through an embryo on the seventh day after impregnation.

Fig. 31. Through anterior part of trunk.

Fig. 32. Through the trunk somewhat behind fig. 31.

Fig. 33. Through tail region.

Fig. 34. Further back than fig. 33, showing constriction of tail from the yolk.

Figs. 35-37. Transverse sections through an embryo on the eighth day after impregnation.

Fig. 35. Through fore-brain and optic vesicles.

Fig. 36. Through hind-brain, showing closed auditory pits, &c.

Fig. 37. Through anterior part of trunk.

Fig. 38. Section through tail of an embryo on the ninth day after impregnation.

PLATE 24.

Fig. 39. Section through the olfactory involution and part of fore-brain of a larva on the ninth day after impregnation, showing olfactory nerve.

Fig. 40. Section through the anterior part of the head of the same larva, showing pituitary involution.

Figs. 41-43. Transverse sections through an embryo on the eleventh day after impregnation.

Fig. 41. Through fore-part of head, showing the pituitary body still connected with the oral epithelium.

Fig. 42. Slightly further back than fig. 41, showing the pituitary body constricted off from the oral epithelium.

Fig. 43. Slightly posterior to fig. 42, to show olfactory involution, eye, and hyomandibular cleft.

Fig. 44. Longitudinal section of the head of an embryo of 15 millims. in length, a few days after hatching, showing the structure of the brain.

Fig. 45. Longitudinal section of the head of an embryo, about five weeks after hatching, 26 millims. in length, showing the structure of the brain. In the front part of the brain the section passes slightly to one side of the median line.

Figs. 46 A to 46 G. Transverse sections through the brain of an embryo 25 millims. in length, about a month after hatching.

Fig. 46 A. Through anterior lobes of cerebrum.

Fig. 46 B. Through posterior lobes of cerebrum.

Fig. 46 C. Through thalamencephalon.

Fig. 46 D. Through optic thalami and optic chiasma.

Fig. 46 E. Through optic lobes and infundibulum.

Fig. 46 F. Through optic lobes and cerebellum.

Fig. 46 G. Through optic lobes and cerebellum, slightly behind fig. 46 F.

PLATE 25.

Figs. 47 A, B, C. Figures of adult brain.

Fig. 47 A. From the side.

Fig. 47 B. From above.

Fig. 47 C. From below.

Fig. 48. Longitudinal vertical section through the eye of an embryo, about a week after hatching, showing the vascular membrane surrounding the vitreous humour.

Fig. 49. Diagram showing the arrangement of the vessels in the vascular membrane of the vitreous humour of adult eye.

Fig. 50. Capillaries of the same vascular membrane.

Fig. 51. Transverse section through anterior part of trunk of an embryo on the ninth day after impregnation, showing the pronephros and pronephric chamber.

Fig. 52. Transverse section through the region of the stomach of an embryo 15 millims. in length, shortly after hatching, to show the glomerulus and peritoneal funnel of pronephros.

Fig. 53. Transverse section through posterior part of the body of an embryo, about a month after hatching, showing the structure of the mesonephros, the spiral valve, &c.

PLATE 26.

Figs. 54, 55, 56, and 57 are a series of transverse sections through the genital ridge and mesonephros of one side from a larva of 11 centims.

Fig. 54. Section of the lymphatic organ which lies in front of the mesonephros.

Fig. 55. Section near the anterior end of the mesonephros, where the genital sac is completely formed.

Fig. 56. Section somewhat further back, showing the mode of formation of the genital sac.

Fig. 57. Section posterior to the above, the formation of the genital sac not having commenced, and the genital ridge with primitive germinal cells projecting freely into the body-cavity.

Fig. 58 A. View of the testis, mesorchium, and duct of the kidney of the left side of an adult male example of *Lepidosteus*, 60 centims. in length, showing the vasa efferentia and the longitudinal canal at the base of the mesorchium. The kidney ducts have been cut open posteriorly to show the structure of the interior.

Fig. 58 B. Inner aspect of the posterior lobe of the testis from the same example, to show the vasa efferentia forming a network on the face of the testis.

Figs. 59 A and B. Two sections showing the structure and relations of the efferent ducts of the testis in the same example.

Fig. 59 A. Section through the inner aspect of a portion of the testis and mesorchium, to show the network of the vasa efferentia (*n.v.e.*) becoming continuous with the seminal tubes (*s.t.*). The granular matter nearly filling the vasa efferentia and the seminal tubes represents the spermatozoa.

Fig. 59 B. Section through part of the kidney and its duct and the longitudinal canal (*l.c.*) at the base of the mesorchium. Canals (*s.c.*) are seen passing off from the latter, which enter the kidney and join the uriniferous tubuli. Some of the latter (as well as the seminal tubes) are seen to be filled with granular matter, which we believe to be the remains of spermatozoa.

Fig. 60. Diagram of the urinogenital organs of the left side of an adult female example of *Lepidosteus* 100 centims. in length. This figure shows the oviduct (*od.*) continuous with the investment of the ovary, opening at *od'*. into the dilated part of the kidney duct (segmental duct). It also shows the segmental duct and the junction of the latter with its fellow of the right side to form the so-called bladder, this part being represented as cut open. The kidney (*k.*) and lymphatic organ (*ly.*) in front of it are also shown.

PLATE 27.

Fig. 61. Transverse section through the developing pancreas (*p.*) of a larva 11 millims. in length.

Fig. 62. Longitudinal section through portions of the stomach, liver, and duodenum of an embryo about a month after hatching, to show the relations of the pancreas (*p.*) to the surrounding parts.

Fig. 63. External view of portions of the liver, stomach, duodenum, &c., of a young Fish, 11 centims. in length, to show the pancreas (*p.*).

Fig. 64. Transverse section through the anterior part of the trunk of an embryo, about a month after hatching, showing the connexion of the air-bladder with the throat (*a.b'*).

Fig. 65. Transverse section through the same embryo as fig. 64 further back, showing the posterior part of the air-bladder (*a.b.*).

Fig. 66. Viscera of an adult female, 100 centims. in length, showing the alimentary canal with its appended glands in natural position, and the air-bladder with its aperture into the throat (*a.b'*). The proximal part of the duodenum and the terminal part of the intestine are represented as cut open, the former to show the pyloric valve and the apertures of the pyloric cæca and bile duct, and the latter to show the spiral valve.

This figure was drawn for us by Professor A. C. HADDON.

PLATE 28.

Fig. 67. Transverse section through the tail of an advanced larva, showing the neural and hæmal processes, the independently developed interneural and inter-hæmal elements (*i.s.*), and the commencing dermal fin-rays (*d.f.*).

Fig. 68. Side view of the tail of a larva, 21 millims. in length, dissected so as to show the structure of the skeleton.

Fig. 69. Longitudinal horizontal section through the vertebral column of a larva, 5.5 centims. in length, on the level of the hæmal arches, showing the intervertebral rings of cartilage continuous with the arches, the vertebral constriction of the notochord, &c.

Figs. 70 and 71. Transverse sections through the vertebral column of a larva of 5.5 centims. The red represents bone, and the blue cartilage.

Fig. 70. Through the vertebral region, showing the neural and hæmal arches, the notochordal sheath, &c.

Fig. 71. Through the intervertebral region, showing the intervertebral cartilage.

Figs. 72 and 73. Transverse sections through the trunk of a larva of 5.5 centims. to show the structure of the ribs and hæmal arches.

Fig. 72. Through the anterior part of the trunk.

Fig. 73. Through the posterior part of the trunk.

PLATE 29.

Figs. 74-76. Transverse sections through the trunk of the same larva as figs. 72 and 73.

Fig. 74. Through the posterior part of the trunk (rather further back than fig. 73).

Fig. 75. Through the anterior part of the tail.

Fig. 76. Rather further back than fig. 75.

- Fig. 77. Longitudinal horizontal section through the vertebral column of a larva of 11 centims., passing through the level of the hæmal arches, and showing the intervertebral constriction of the notochord, the ossification of the cartilage, &c.
- Fig. 78. Transverse section through a vertebral region of the vertebral column of a larva 11 centims. in length.
- Fig. 79. Transverse section through an intervertebral region of the same larva as fig. 78.
- Fig. 80. Side view of two trunk vertebræ of an adult *Lepidosteus*.
- Fig. 81. Front view of a trunk vertebra of adult.

In figures 80 and 81 the red does not represent bone as in the other figures, but simply the ligamentum longitudinale superius.

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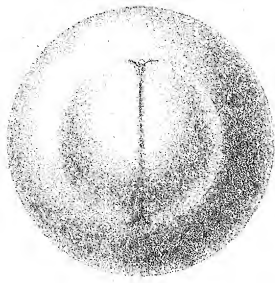


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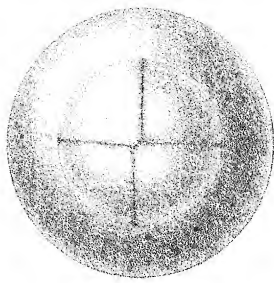


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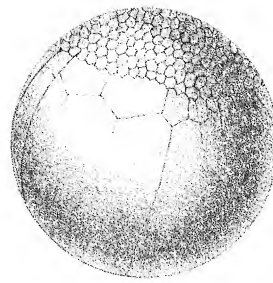


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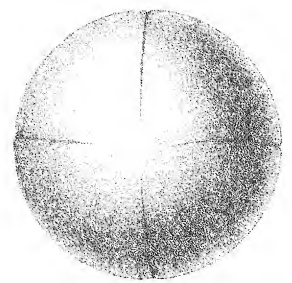


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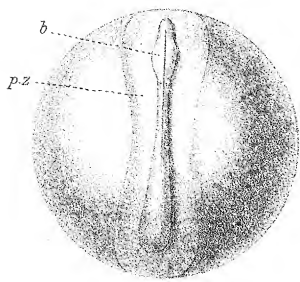


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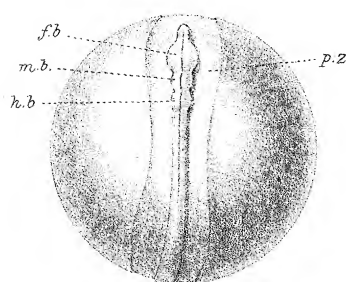


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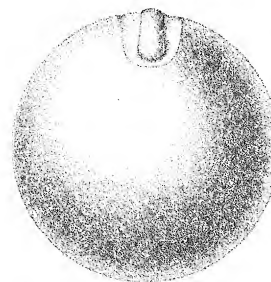


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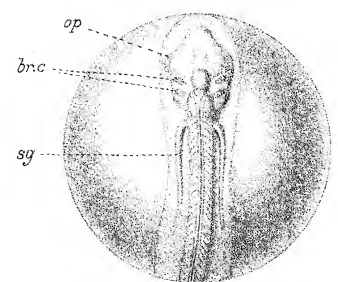


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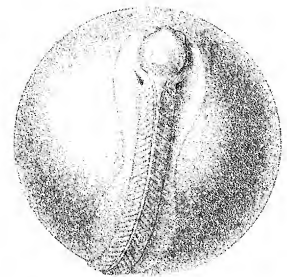


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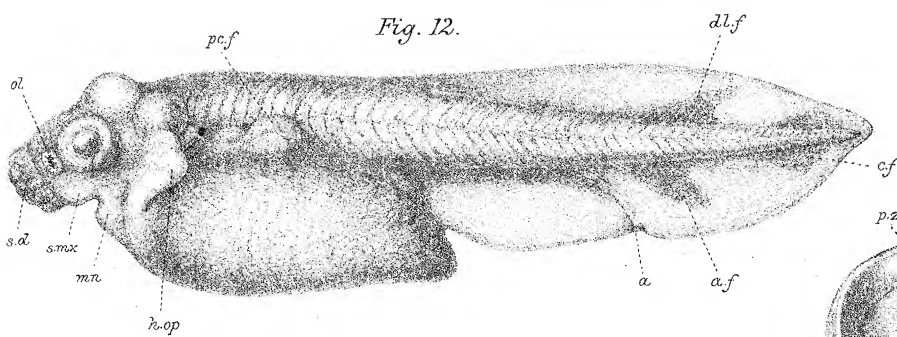


Fig. 10.

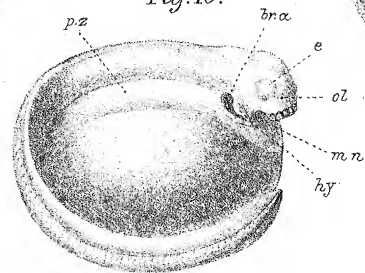


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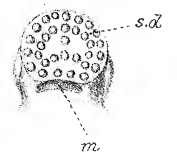


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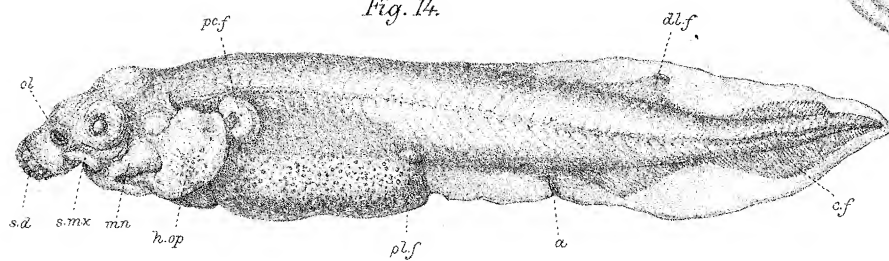


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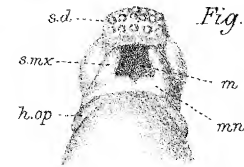


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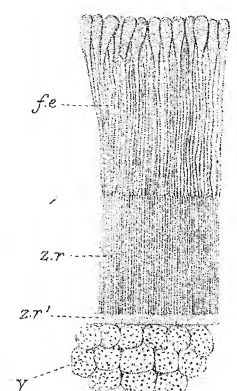


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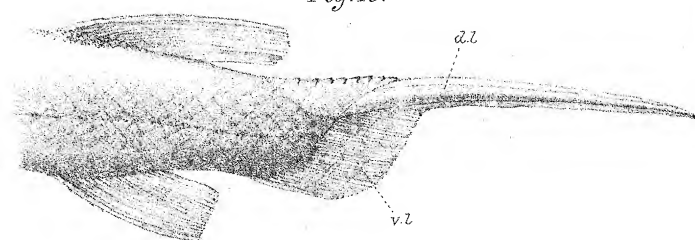
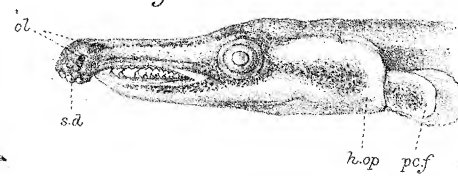
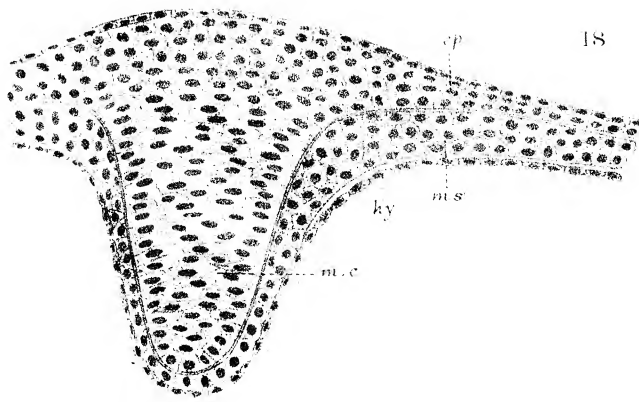
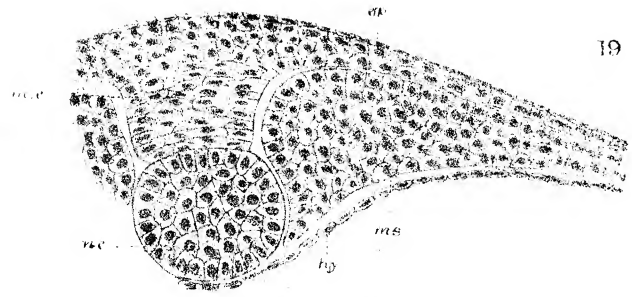


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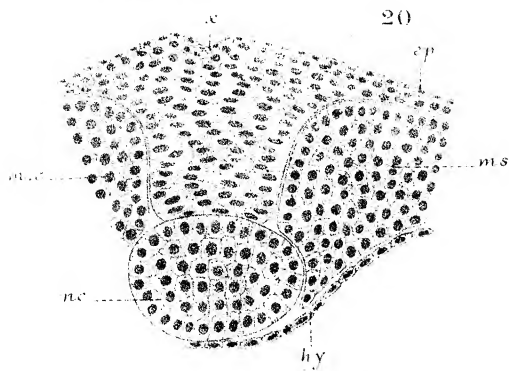




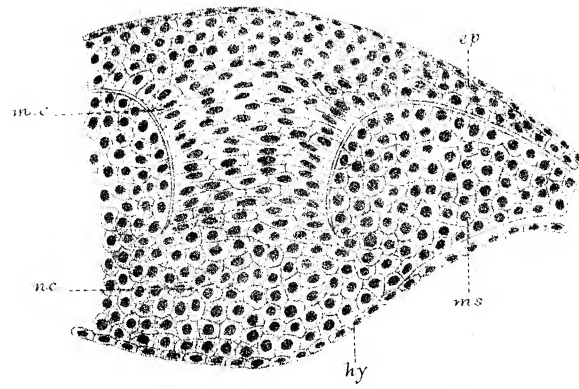
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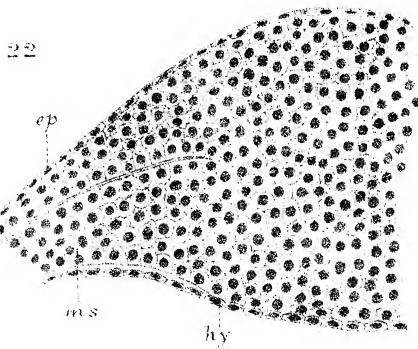
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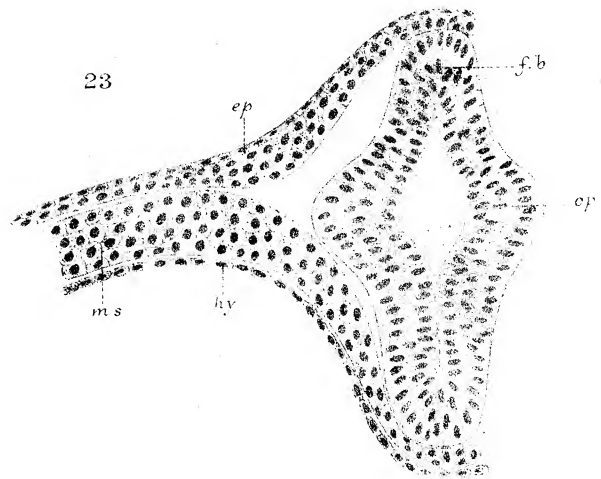
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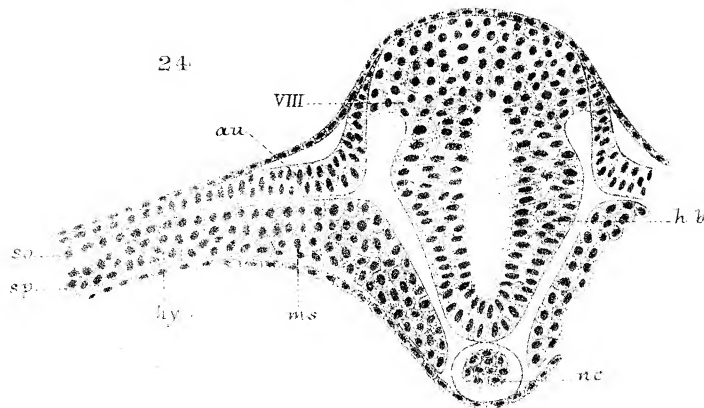
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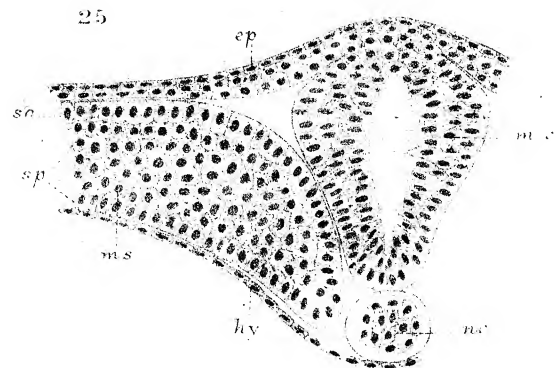
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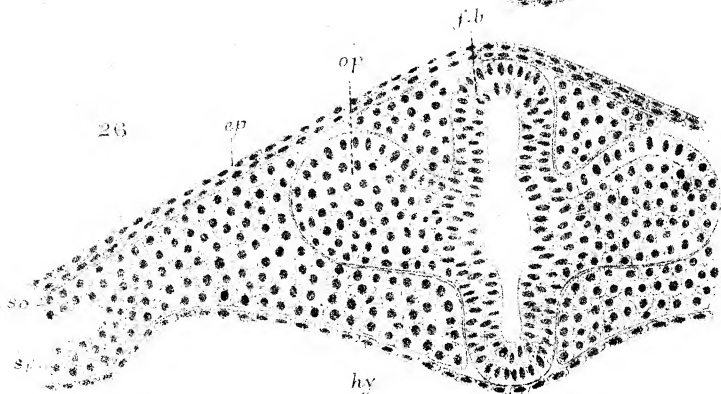
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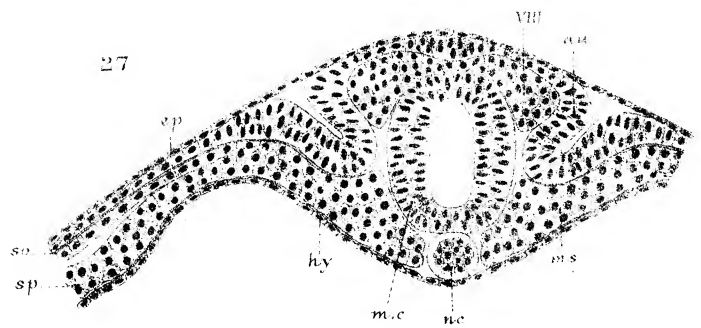
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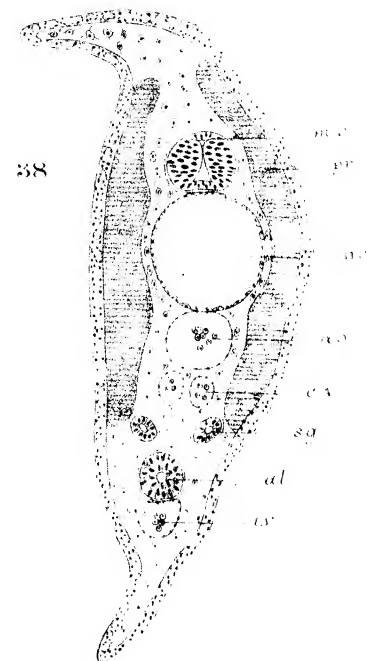
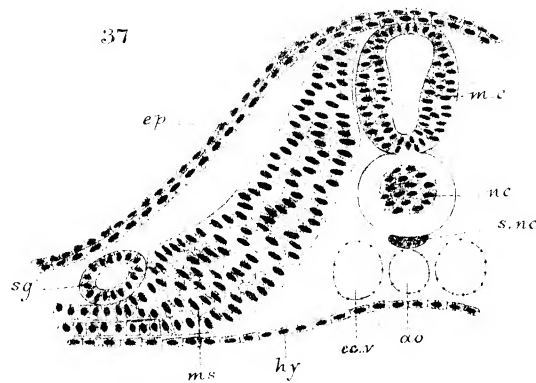
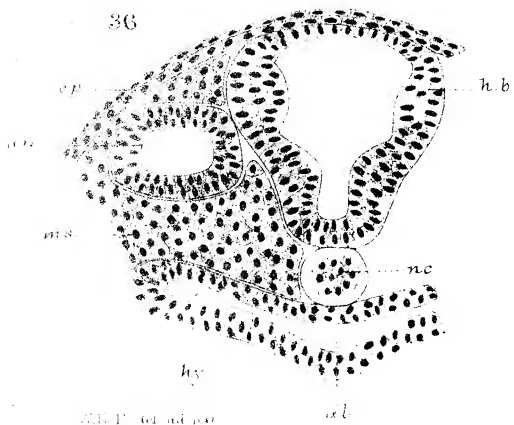
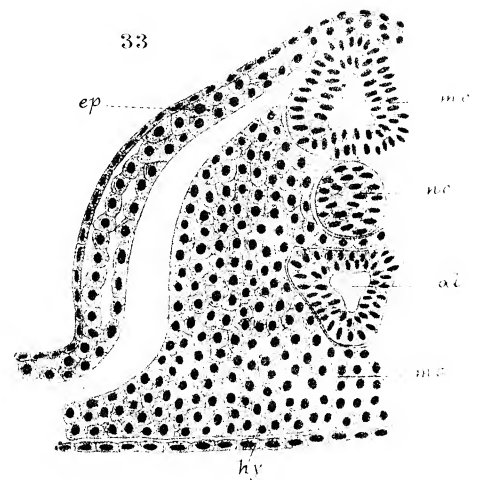
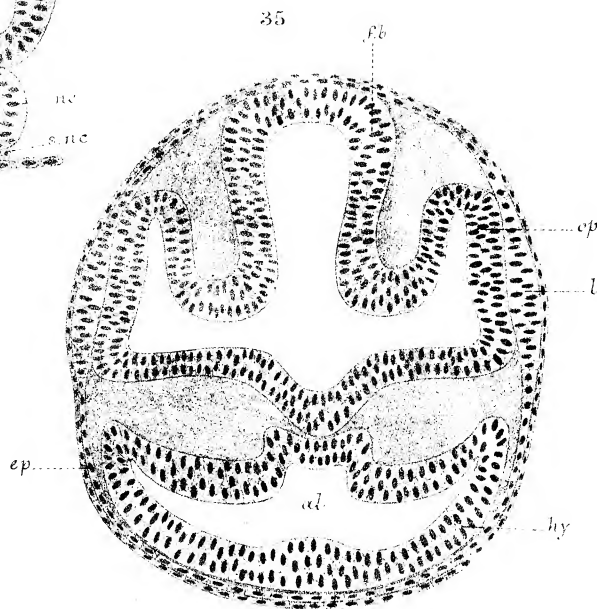
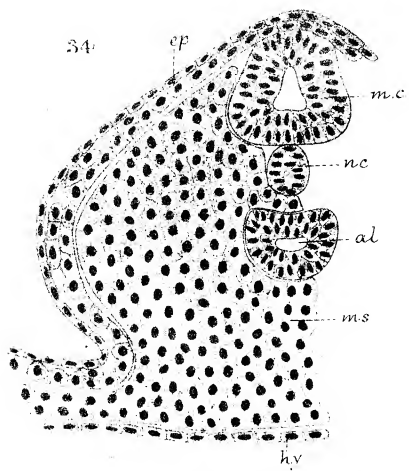
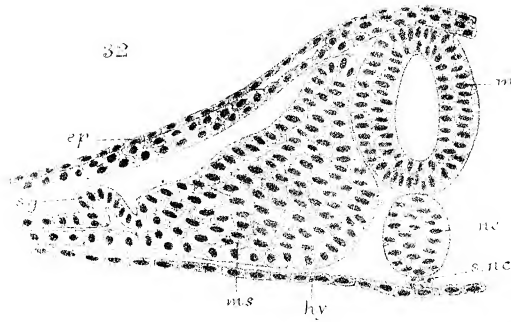
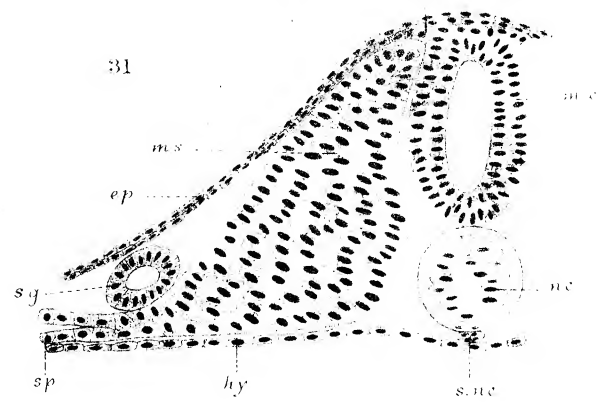
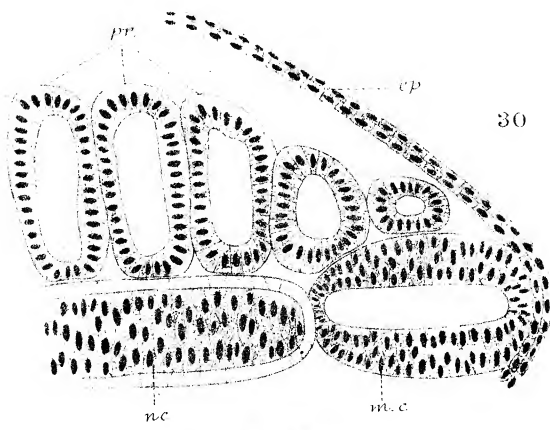
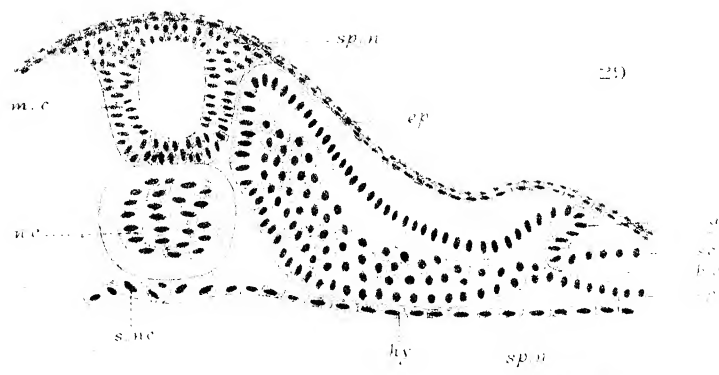
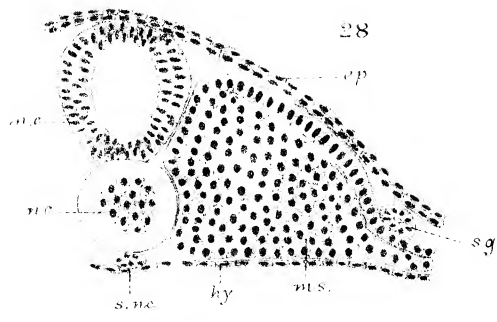


Fig. 39.

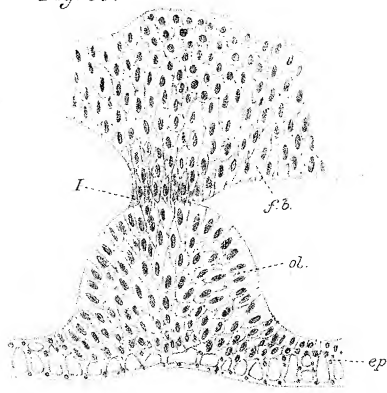


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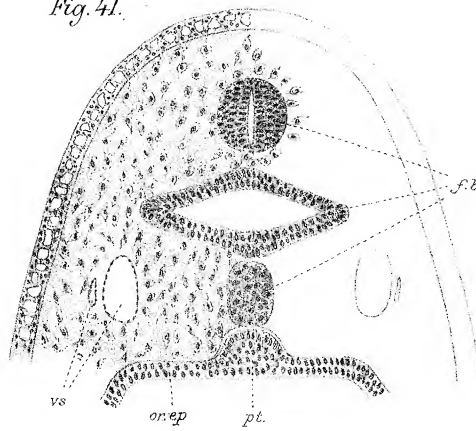


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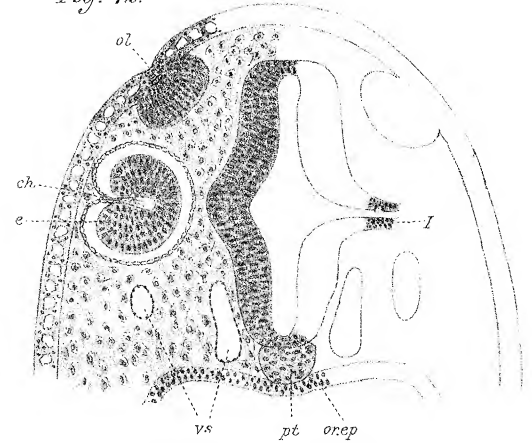


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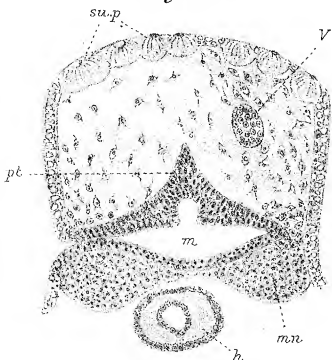


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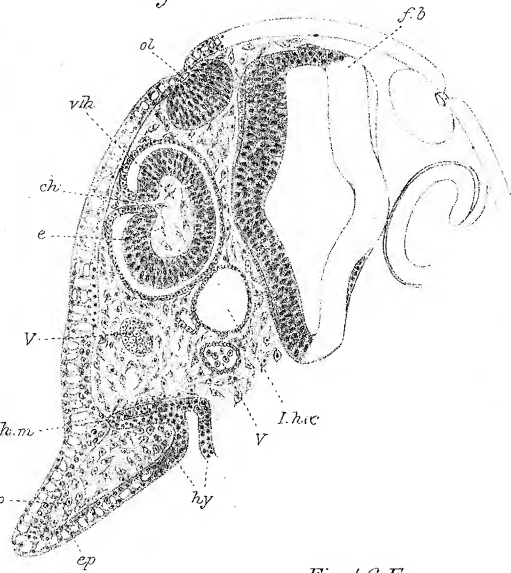


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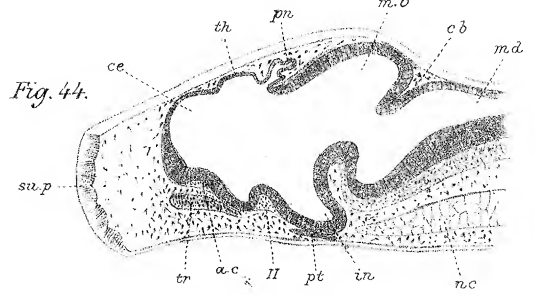


Fig. 46 A.



Fig. 46 B.

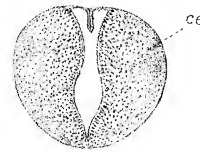


Fig. 46 C.

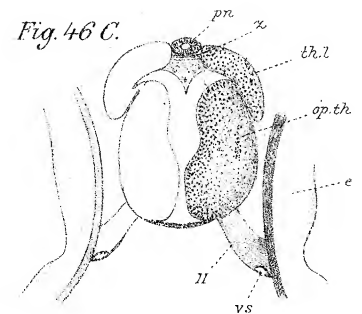


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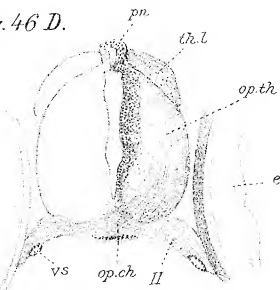


Fig. 46 E.

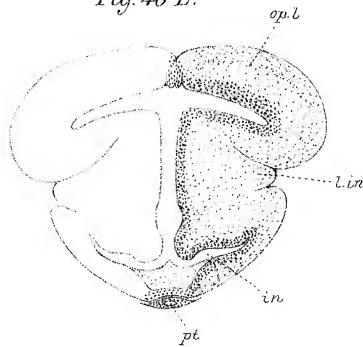


Fig. 46 F.

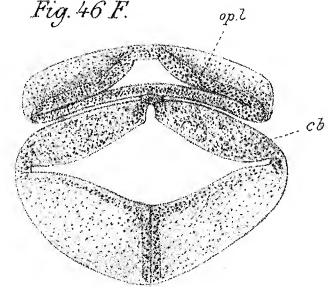


Fig. 46 G.

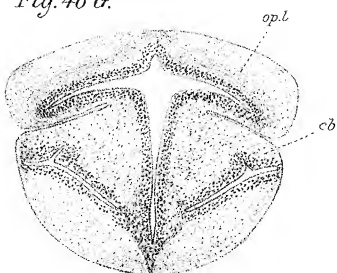
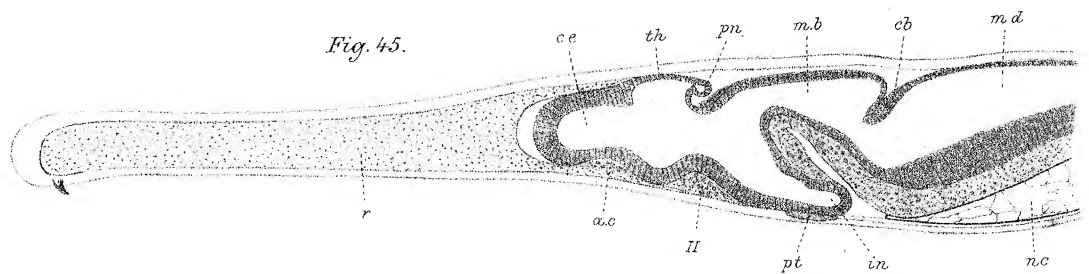


Fig. 45.



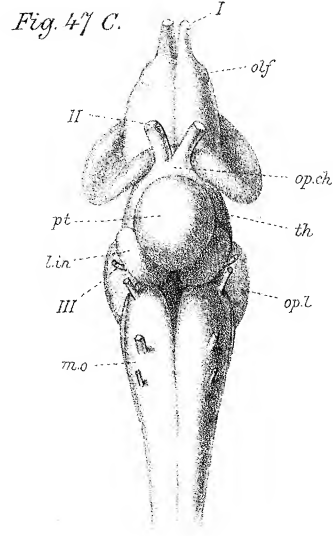
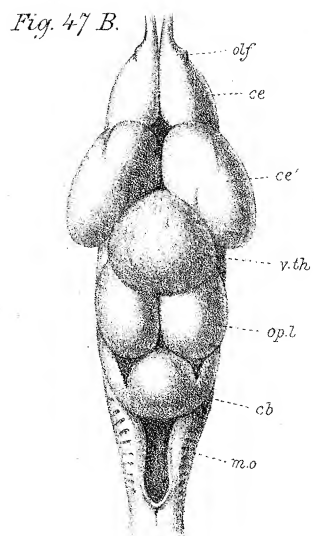
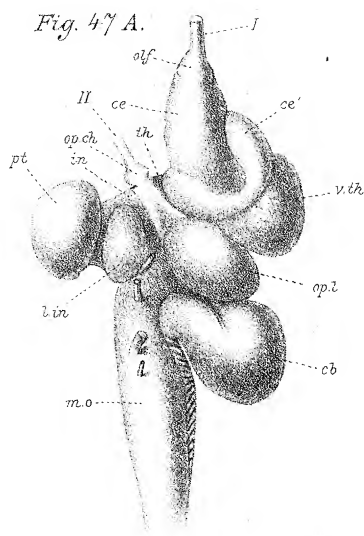


Fig. 50.

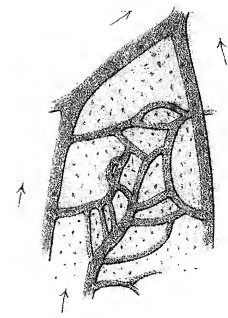


Fig. 48.

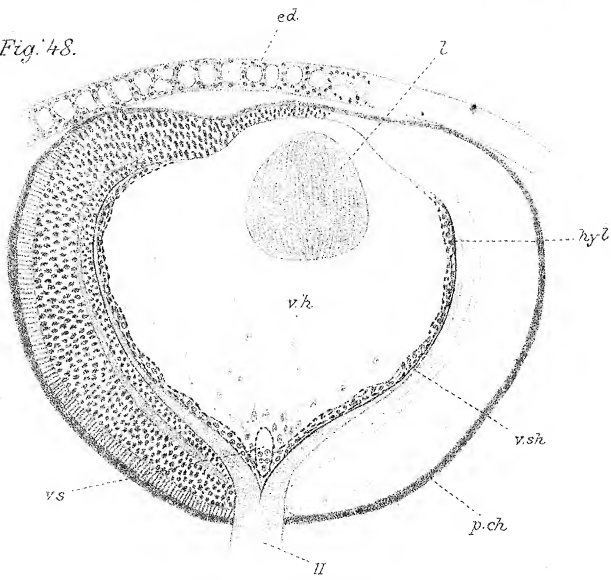


Fig. 49.

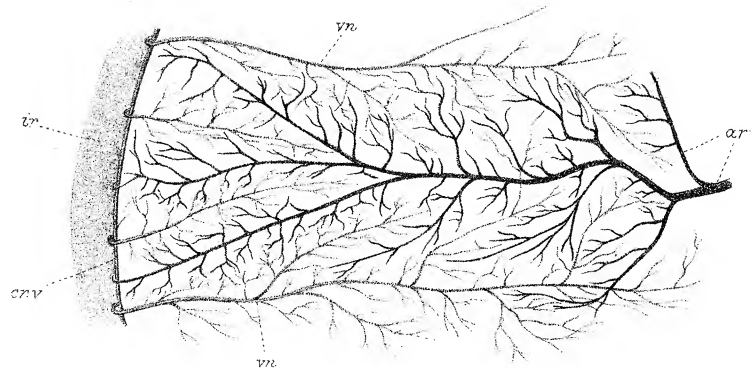


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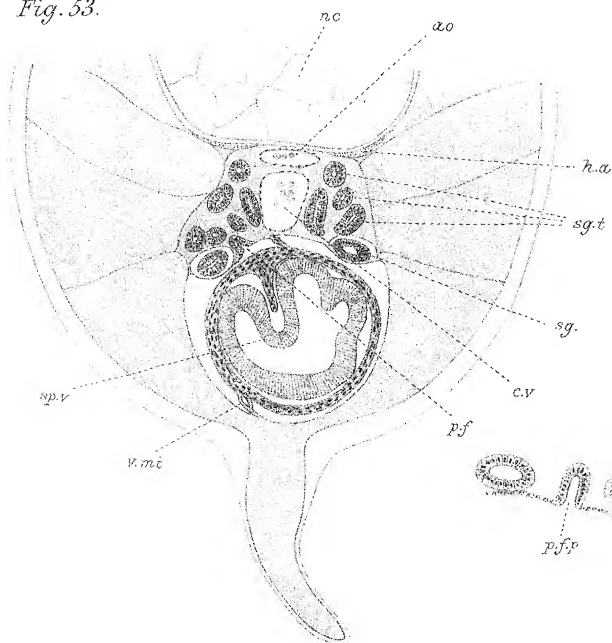


Fig. 51.

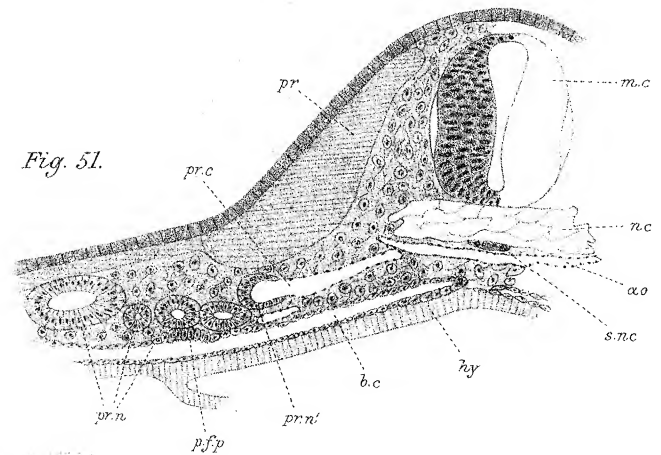


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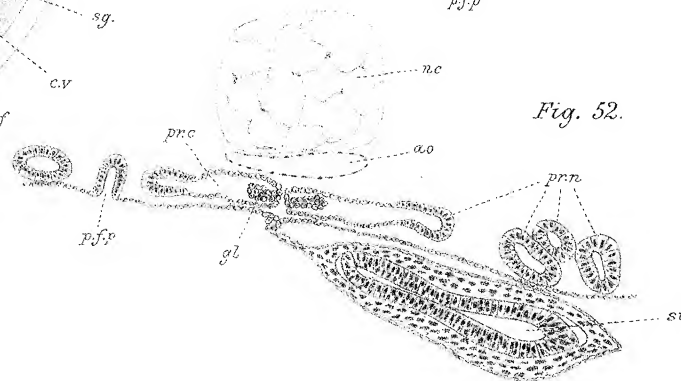


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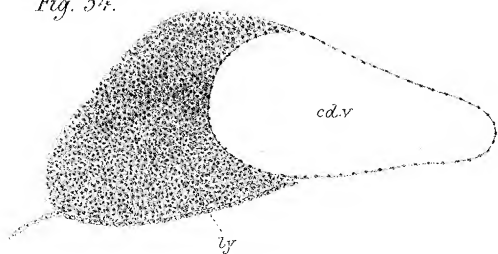


Fig. 55.

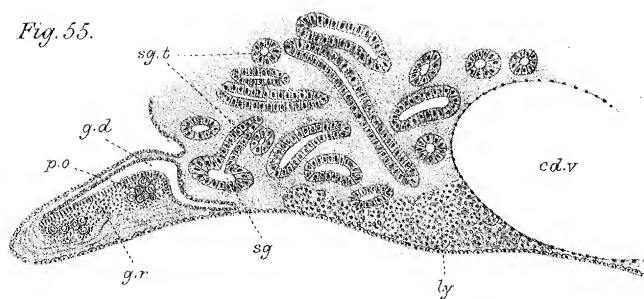


Fig. 56.

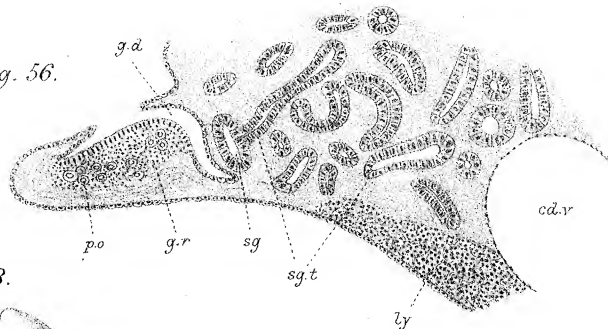


Fig. 57.

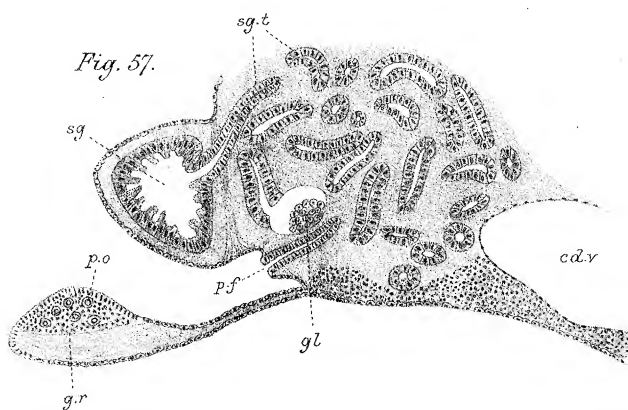


Fig. 58B.

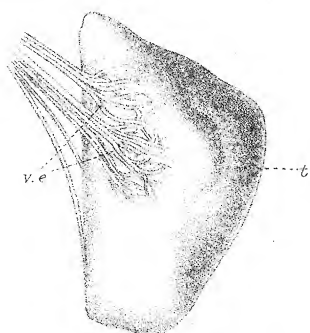


Fig. 58A.

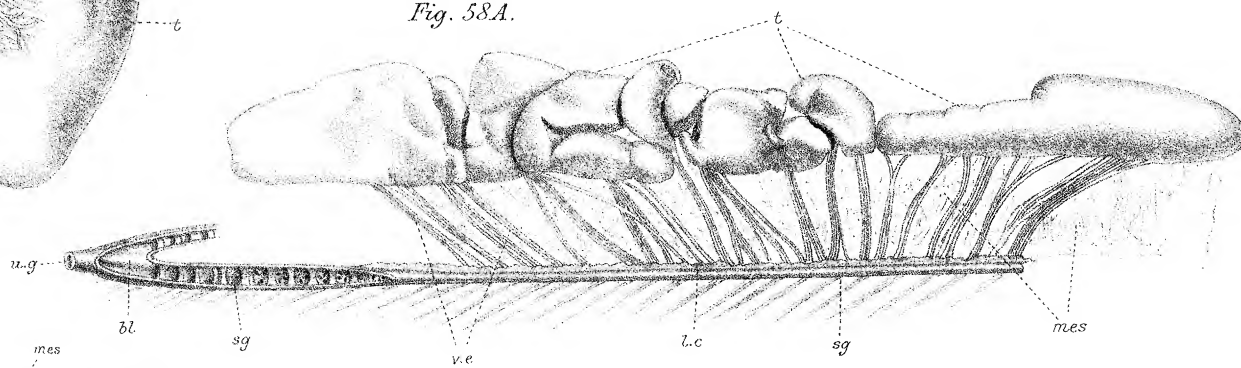


Fig. 59B.

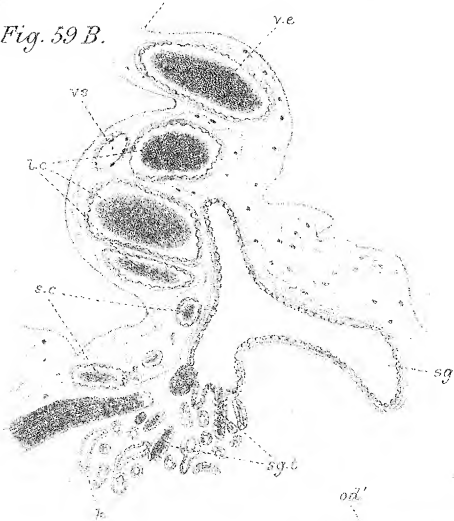


Fig. 59A.

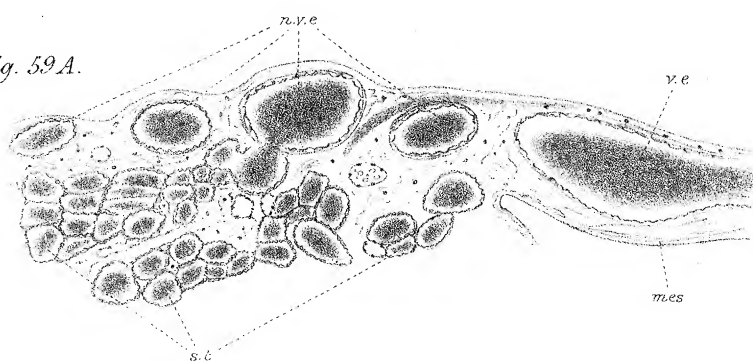
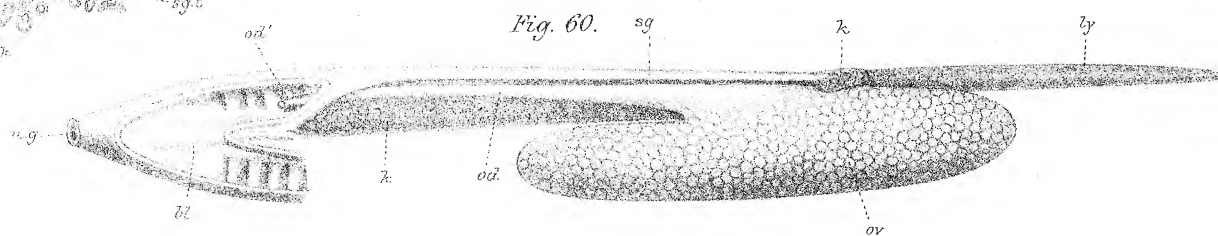


Fig. 60.



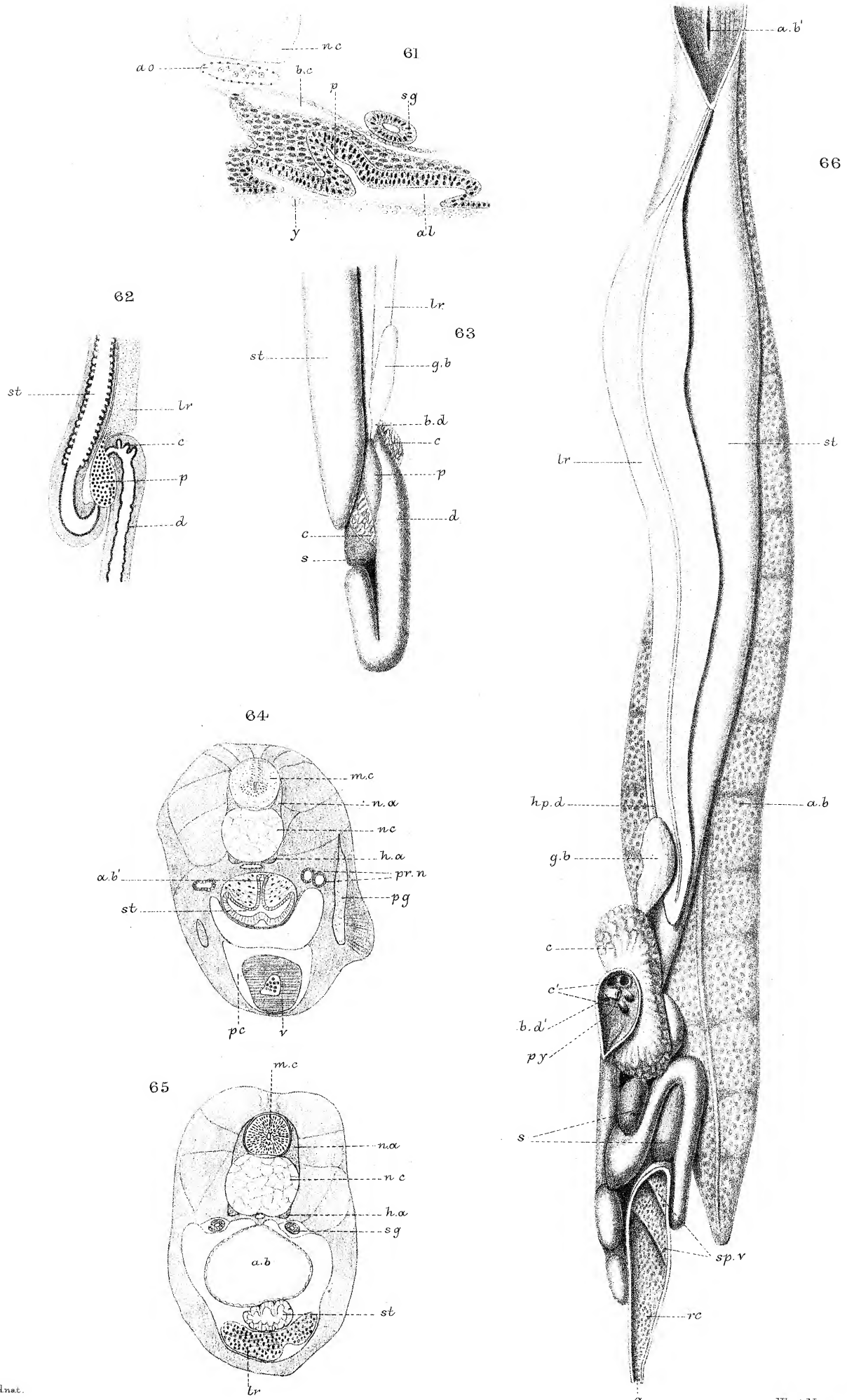


Fig. 67.

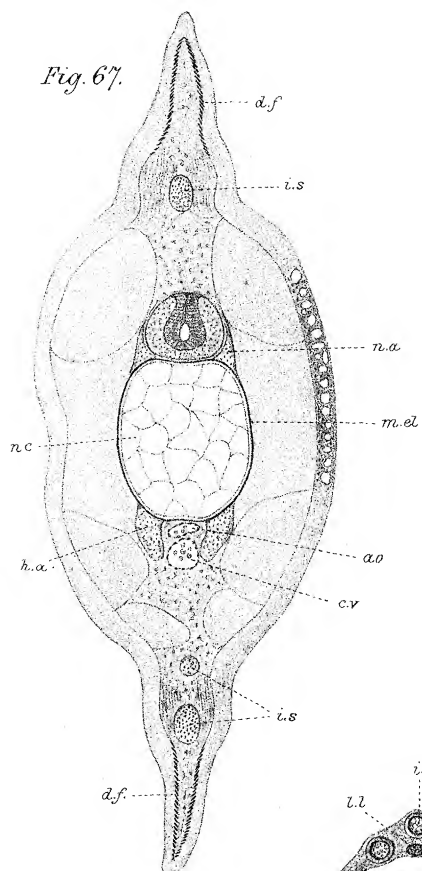


Fig. 68.

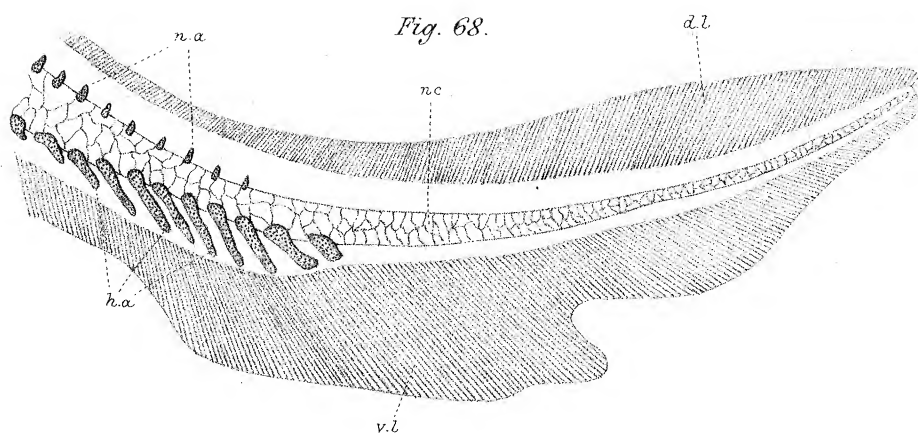


Fig. 69.

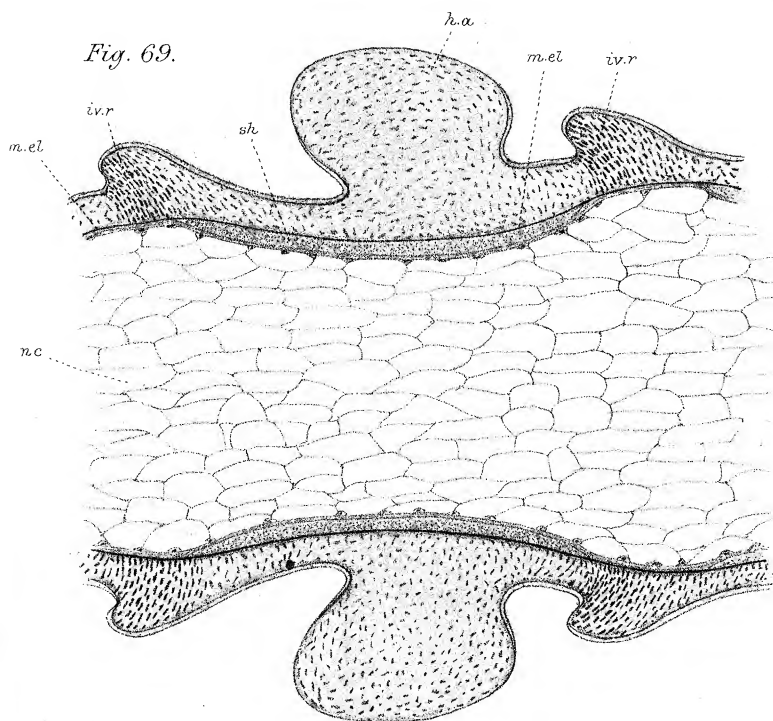


Fig. 70.

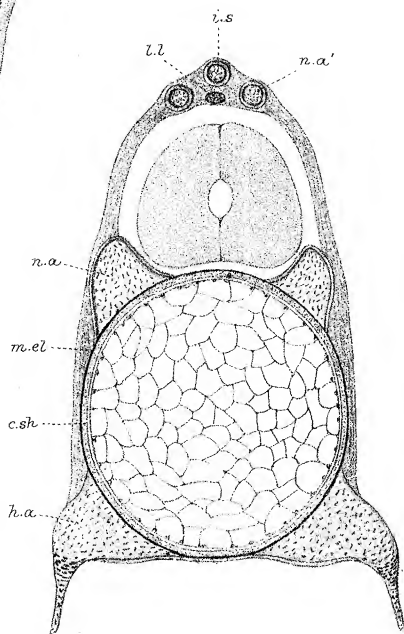


Fig. 71.

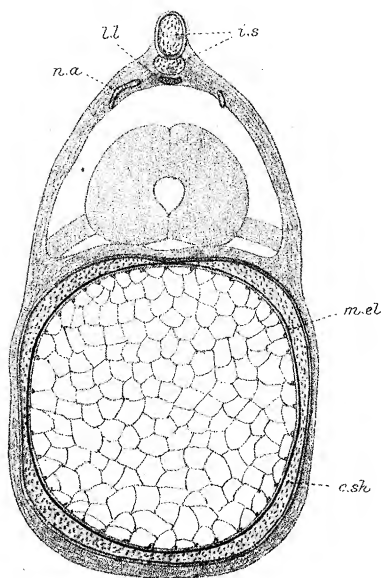


Fig. 73.

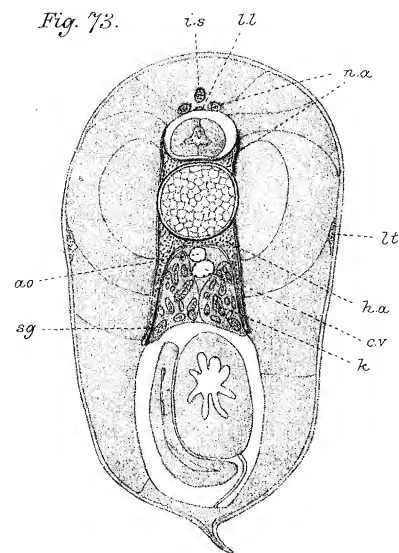
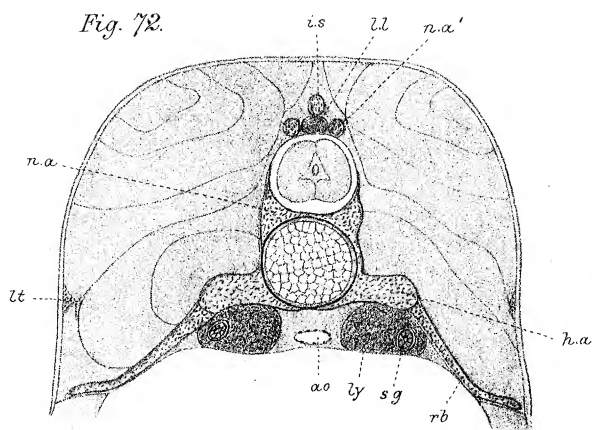


Fig. 72.



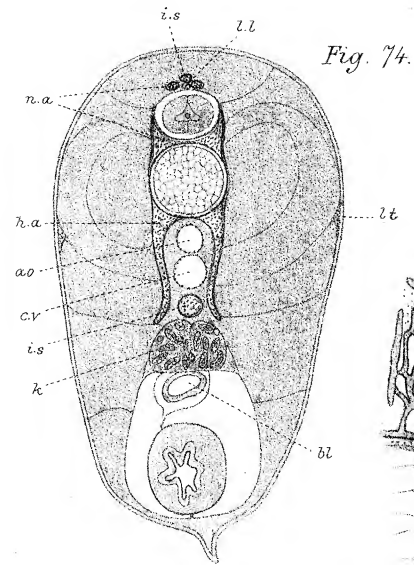


Fig. 74.

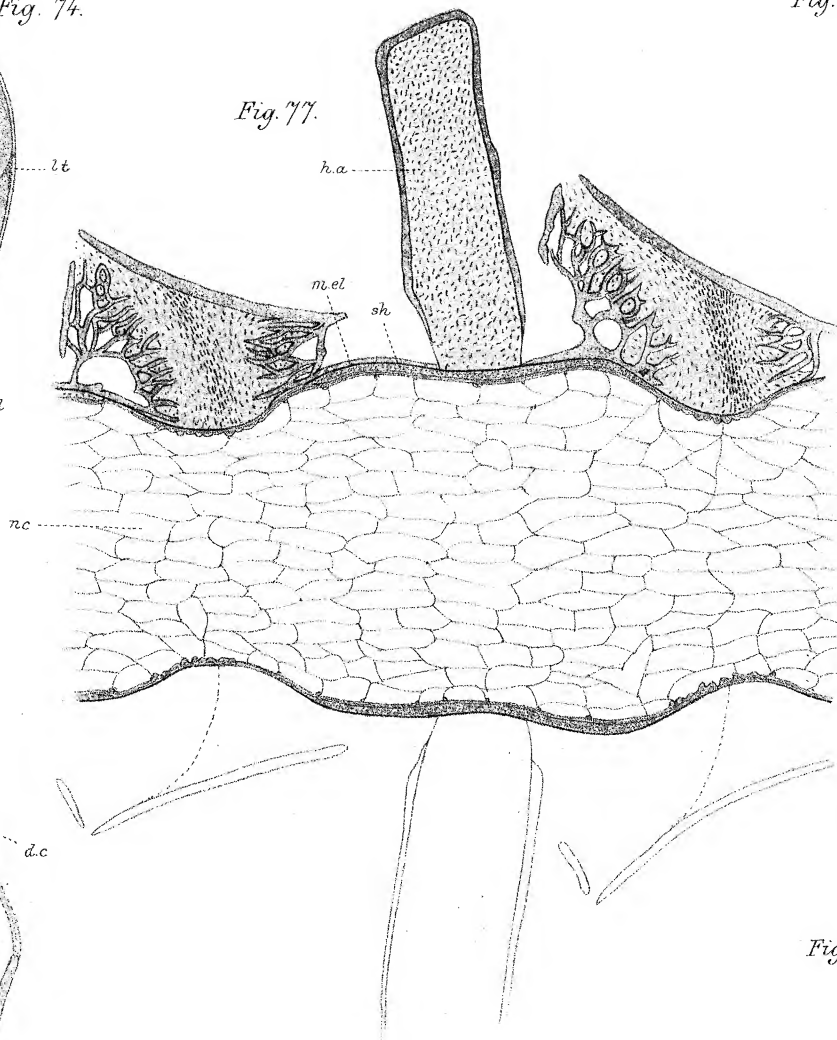


Fig. 77.

Fig. 75.

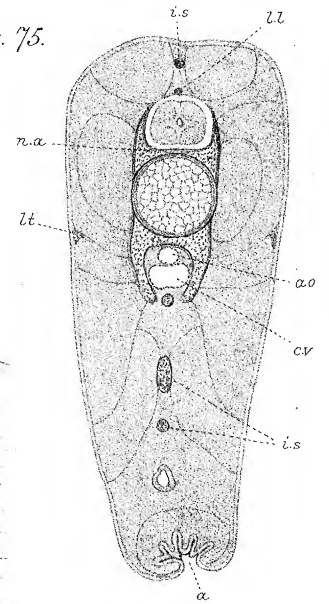


Fig. 76.

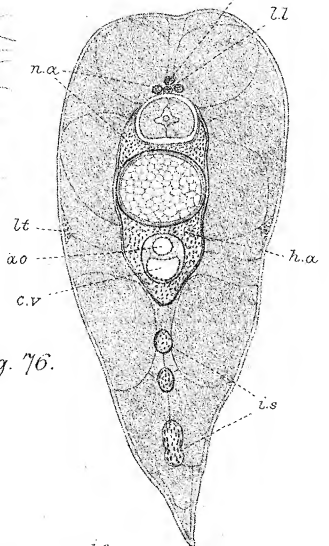


Fig. 79.

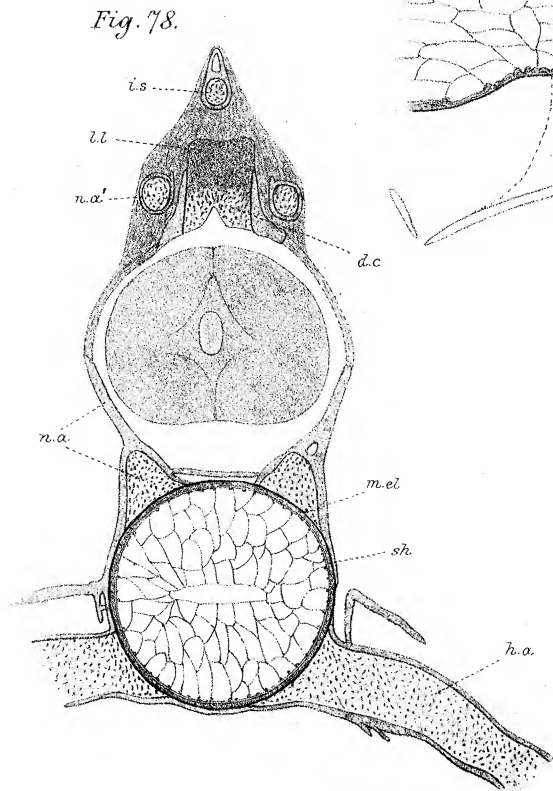
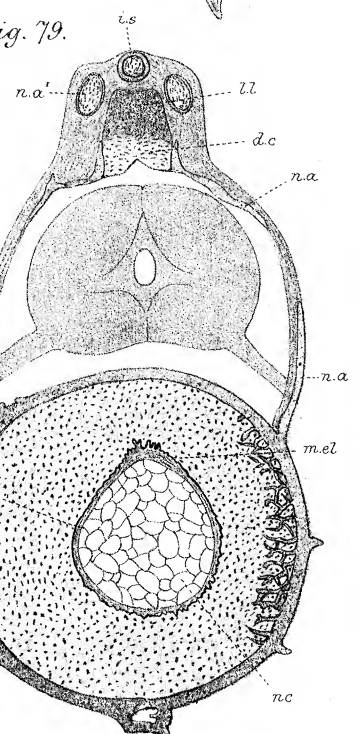


Fig. 78.

Fig. 80.

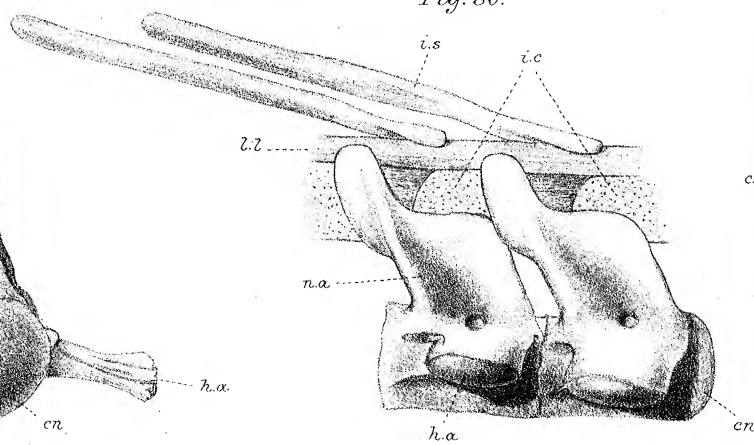


Fig. 81.

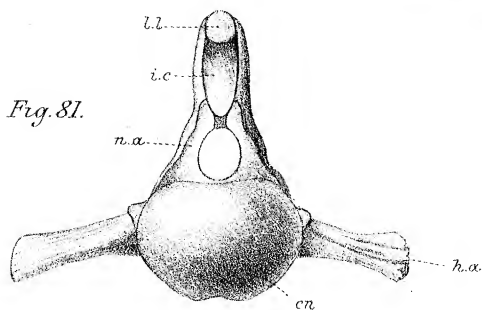




PLATE 23.

Figs. 28-29. Transverse sections of the trunk of an embryo on the sixth day after impregnation.

Fig. 28. Through anterior part of trunk (from a slightly older embryo than the other sections of this stage).

Fig. 29. Slightly posterior to fig. 28, showing formation of segmental duct as a fold of the somatic mesoblast.

Fig. 30. Longitudinal horizontal section of embryo on the sixth day after impregnation, passing through the mesoblastic somites, notochord, and medullary canal.

Figs. 31-34. Transverse sections through an embryo on the seventh day after impregnation.

Fig. 31. Through anterior part of trunk.

Fig. 32. Through the trunk somewhat behind fig. 31.

Fig. 33. Through tail region.

Fig. 34. Further back than fig. 33, showing constriction of tail from the yolk.

Figs. 35-37. Transverse sections through an embryo on the eighth day after impregnation.

Fig. 35. Through fore-brain and optic vesicles.

Fig. 36. Through hind-brain, showing closed auditory pits, &c.

Fig. 37. Through anterior part of trunk.

Fig. 38. Section through tail of an embryo on the ninth day after impregnation.

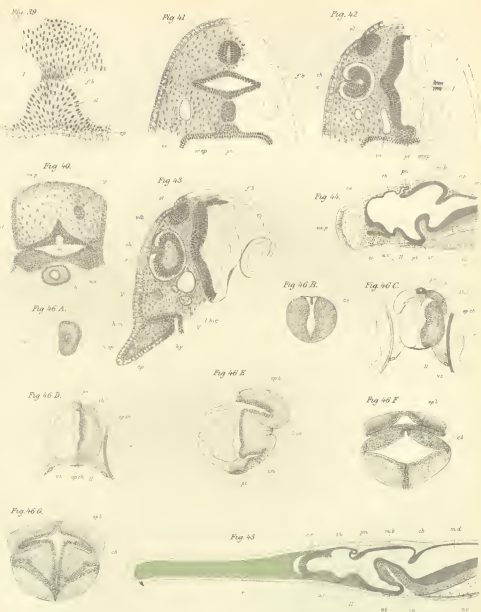


PLATE 24.

Fig. 39. Section through the olfactory involution and part of fore-brain of a larva on the ninth day after impregnation, showing olfactory nerve.

Fig. 40. Section through the anterior part of the head of the same larva, showing pituitary involution.

Figs. 41-43. Transverse sections through an embryo on the eleventh day after impregnation.

Fig. 41. Through fore-part of head, showing the pituitary body still connected with the oral epithelium.

Fig. 42. Slightly further back than fig. 41, showing the pituitary body constricted off from the oral epithelium.

Fig. 43. Slightly posterior to fig. 42, to show olfactory involution, eye, and hyomandibular cleft.

Fig. 44. Longitudinal section of the head of an embryo of 15 millims. in length, a few days after hatching, showing the structure of the brain.

Fig. 45. Longitudinal section of the head of an embryo, about five weeks after hatching, 26 millims. in length, showing the structure of the brain. In the front part of the brain the section passes slightly to one side of the median line.

Figs. 46 A to 46 G. Transverse sections through the brain of an embryo 25 millims. in length, about a month after hatching.

Fig. 46 A. Through anterior lobes of cerebrum.

Fig. 46 B. Through posterior lobes of cerebrum.

Fig. 46 C. Through thalamencephalon.

Fig. 46 D. Through optic thalami and optic chiasma.

Fig. 46 E. Through optic lobes and infundibulum.

Fig. 46 F. Through optic lobes and cerebellum.

Fig. 46 G. Through optic lobes and cerebellum, slightly behind fig. 46 F.

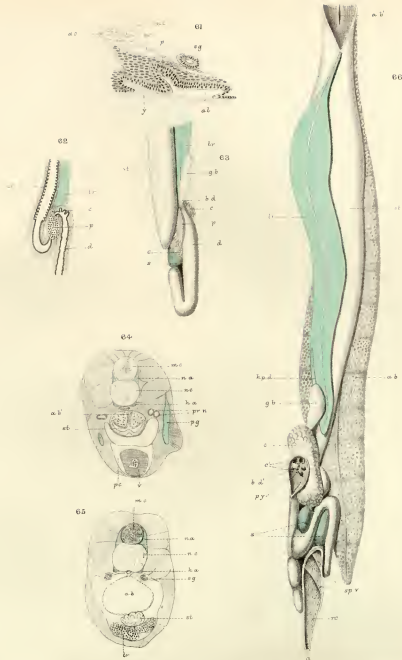


PLATE 27.

- Fig. 61. Transverse section through the developing pancreas (*p*) of a larva 11 millims. in length.
- Fig. 62. Longitudinal section through portions of the stomach, liver, and duodenum of an embryo about a month after hatching, to show the relations of the pancreas (*p*) to the surrounding parts.
- Fig. 63. External view of portions of the liver, stomach, duodenum, &c., of a young Fish, 11 centims. in length, to show the pancreas (*p*).
- Fig. 64. Transverse section through the anterior part of the trunk of an embryo, about a month after hatching, showing the connexion of the air-bladder with the throat (*a.b.*).
- Fig. 65. Transverse section through the same embryo as fig. 64 further back, showing the posterior part of the air-bladder (*a.b.*).
- Fig. 66. Viscera of an adult female, 100 centims. in length, showing the alimentary canal with its appended glands in natural position, and the air-bladder with its aperture into the throat (*a.b.*). The proximal part of the duodenum and the terminal part of the intestine are represented as cut open, the former to show the pyloric valve and the apertures of the pyloric caeca and bile duct, and the latter to show the spiral valve.

This figure was drawn for us by Professor A. C. HADDON.

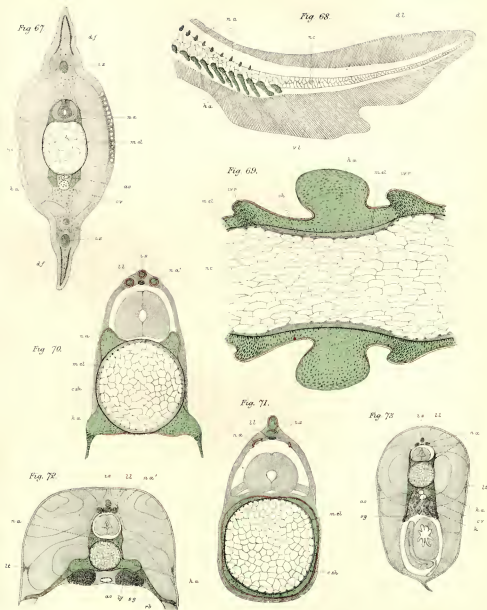


PLATE 28.

Fig. 67. Transverse section through the tail of an advanced larva, showing the neural and hæmal processes, the independently developed interneural and inter-hæmal elements (*i.s.*), and the commencing dermal fin-rays (*d.f.*).

Fig. 68. Side view of the tail of a larva, 21 millims. in length, dissected so as to show the structure of the skeleton.

Fig. 69. Longitudinal horizontal section through the vertebral column of a larva, 5.5 centims. in length, on the level of the hæmal arches, showing the intervertebral rings of cartilage continuous with the arches, the vertebral constriction of the notochord, &c.

Figs. 70 and 71. Transverse sections through the vertebral column of a larva of 5.5 centims. The red represents bone, and the blue cartilage.

Fig. 70. Through the vertebral region, showing the neural and hæmal arches, the notochordal sheath, &c.

Fig. 71. Through the intervertebral region, showing the intervertebral cartilage.

Figs. 72 and 73. Transverse sections through the trunk of a larva of 5.5 centims. to show the structure of the ribs and hæmal arches.

Fig. 72. Through the anterior part of the trunk.

Fig. 73. Through the posterior part of the trunk.

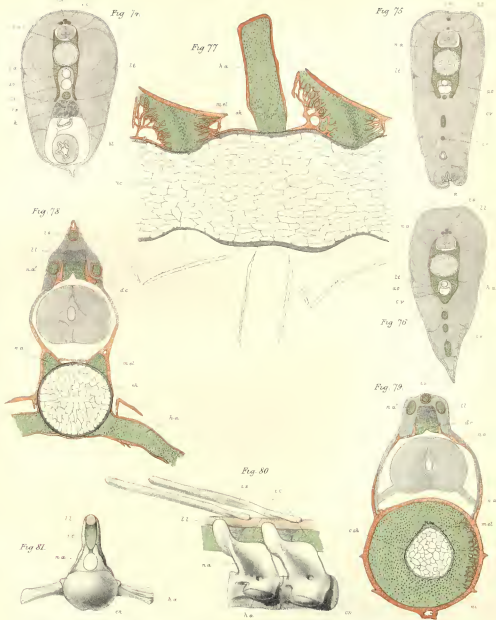


PLATE 29.

Figs. 74-76. Transverse sections through the trunk of the same larva as figs. 72 and 73.

Fig. 74. Through the posterior part of the trunk (rather further back than fig. 73).

Fig. 75. Through the anterior part of the tail.

Fig. 76. Rather further back than fig. 75.

Fig. 77. Longitudinal horizontal section through the vertebral column of a larva of 11 centims., passing through the level of the hemal arches, and showing the intervertebral constriction of the notochord, the ossification of the cartilage, &c.

Fig. 78. Transverse section through a vertebral region of the vertebral column of a larva 11 centims. in length.

Fig. 79. Transverse section through an intervertebral region of the same larva as fig. 78.

Fig. 80. Side view of two trunk vertebrae of an adult *Lepidosteus*.

Fig. 81. Front view of a trunk vertebra of adult.

In figures 80 and 81 the red does not represent bone as in the other figures, but simply the ligamentum longitudinale superius.